A comparative analysis of the wrist and ankle morphology of hominoids and lorisids, with implications for the evolution of hominoid locomotion

Read, Catriona S.

A Comparative Analysis of the Wrist and Ankle Morphology of Hominoids and Lorisids, with Implications for the Evolution of Hominoid Locomotion

A Dissertation presented

by

Catriona S. Read

to

The Graduate School

For the degree of

Master of Science

in

Biological Anthropology

Department of Anthropology

University of Durham

September 2001

Declaration

This thesis is the result of my own work, and no part of it has previously been submitted for a degree at any University. Material from the published or unpublished work of others, which is referred to in the thesis, is credited to the source in the text.

Abstract of the Dissertation

A Comparative Analysis of the Wrist and Ankle Morphology of Hominoids and Lorisids, with Implications for the Evolution of Hominoid Locomotion

by

Catriona S. Read

in

Biological Anthropology

Department of Anthropology
University of Durham

October 2001

There has been considerable debate concerning the adaptive significance of hominoid postcranial anatomy. One of the hypotheses promoted is that the early hominoids were adapted to a loris-like deliberate quadrupedalism. The aim of the analysis reported here is to test this hypothesis by examining features of the wrist and ankle anatomy of lorisids and hominoids that pertain to increased joint mobility, in a comparative context with other arboreal quadrupeds. These characters are then compared with the Proconsulidae from the early Miocene to discern any similarities between these taxa and the lorisids and/or hominoids.

Fourteen characters were examined, related to the ulnocarpal and radioulnar articulations, and the talocrural, subtalar and midtarsal joints, across four lorisid and four hominoid genera, and a selection of primates from the other major groups. Original measurements were taken for two hundred and twenty-nine neontological specimens in total, from fourteen genera. Indices were devised and compared by statistical analysis.

The results suggest that lorisids and hominoids are similar in some of the characters examined, but differ in others. The proconsulids show varying degrees of similarity across the features, to the hominoids and lorisids. The results support a hypothesis that an early hominoid ancestor did indeed have similar functional adaptations to those of extant lorisids, but not across the whole suite of characters examined. It is therefore reasonable to assume that the ancestral hominoid locomotor pattern showed resemblances to that of the extant lorisids, but was not identical.

Acknowledgements

I would like to take this opportunity to thank those who assisted me during the course this study. Firstly, I thank Bob Randall at the American Museum of Natural History, New York, and Linda Gordon at the National Museum of Natural History, Washington D. C. for allowing me access to the extant primate collections in their care, and for the assistance provided by themselves and their staff during my visits. I would also like to thank John Langdon, Department of Biology at the University of Indianapolis, who very kindly allowed me access to his unpublished fossil data, without which much of the fossil inference would have been impossible. My thanks go especially to my supervisor, Todd C. Rae, for his constant advice and support throughout this study, and most particularly for keeping me focused when things did not go exactly to plan. It is primarily due to Todd that I developed my current interests, and his apparent faith in me has been very encouraging. Finally, I would like to thank my family, who have been hugely supportive throughout, and Calum, who has shown extreme tolerance of, and amusement at, his Mummy's unusual interests.

Table of Contents

Table of Figures

CHAPTER 1

Introduction

OBJECTIVES

As a group hominoids possess a suite of postcranial synapomorphies in the forelimb, hindlimb, thorax, pelvis and vertebral column, and these characteristics can be related to the postural and locomotor behaviour of these genera (MacLatchy and Bossert, 1996; Harrison, 1987). Due to the apparent cohesive nature of this group in terms of its postcranial morphology, it is reasonable to assume that these taxa derive from a common morphological, and hence behavioural, base. Various studies have proposed a number of hypotheses for a basal hominoid locomotor type, ranging from the specialised brachiation or knucklewalking behaviours seen in the extant forms, to vertical climbing, or slow quadrupedal types (e.g., Lewis, 1971a, 1972a-b, 1974; Conroy and Fleagle, 1972; Cartmill and Milton, 1977; Fleagle et al., 1981; Gebo, 1996).

Despite the superficial uniformity in locomotor anatomy of the extant hominoids, however, these taxa are quite diverse in their positional behaviour (Tuttle, 1986), and possess structural differences in their postcrania that reflect these contrasting behavioural adaptations (Ward, 1998). Whilst analysts have attempted to categorise the extant forms under all-encompassing terms such as 'suspensory' or 'brachiators' (e.g., Ashton and Oxnard, 1964; Napier and Napier, 1967), these definitions are not adequate to reflect the true nature of hominoid behavioural and anatomical diversity. The brachiation of the modern gibbon is very different to the essentially quadrupedal knucklewalking of the African apes, and both are different again to the quadrumanous climbing and bridging behaviour utilised by the orangutan, and human bipedalism. Thus, any underlying locomotor origin must be seen as pre-adaptive for the evolution of all of these modern specialisations.

Furthermore, the wealth of analyses of the earliest hominoids from the Miocene of East Africa suggests that many elements of the postcrania of these genera were

quite different from those seen in the extant apes (e.g., Rose, 1983), but found in combination with undisputed hominoid synapomorphies (e.g., loss of tail [Ward et al., 1991]) The majority of recent studies, however, support a view that the early hominoids were pronograde arboreal quadrupeds (Ward, 1993a-b, 1997, 1998; Strait et al, 2000), which effectively falsifies hypotheses of an orthograde, suspensory or knucklewalking common ancestor.

Thus, the debate about the evolution of hominoid locomotion remains largely unresolved. Any theory must accommodate a relatively primitive, and essentially monkey-like, early Miocene form, and yet must also address the specialisations seen in hominoids today. It is suggested that a common ancestor was a relatively unspecialised arboreal quadruped, with enhanced manual and pedal grasping capabilities, and characterised by slow progression (Aiello, 1981; Conroy and Rose, 1983; Rose, 1983, 1996; Walker & Pickford, 1983; Langdon, 1986; Leakey et al., 1988b; Begun et al., 1994). Remarkably, the closest extant analogues to this form of locomotion are the strepsirrhine lorisids, and indeed these taxa show distinct convergence with the hominoids in certain postcranial characteristics (Cartmill and Milton, 1977).

The primary aim of the thesis is to critically evaluate current theories of early evolution of hominoid locomotion. This is accomplished through an examination of postcranial features in some extant primate taxa. The specific hypothesis addressed is that proposed initially by Cartmill and Milton (1977), and revised by Kelley (1997); that the initial hominoid postcranial adaptation was lorisid-like cautious arboreal quadrupedalism, rather than brachiation, knuckle-walking or vertical climbing. This hypothesis is assessed by means of a comparative analysis of extant primate postcrania, and the functional interpretation of statistical data. Elements of the wrist and ankle joint that have been previously described as synapomorphic hominoid characteristics are analysed, and compared with those exhibited in the slow quadrupedal lorisids and in other arboreal quadrupeds. If the lorises exhibit similar adaptations of these specific regions to extant hominoids, to the exclusion of other arboreal primates, it might be inferred that they are homoplastic characteristics, evolved to perform the same functional role.

In view of the fact that lorises do not engage in the three alternative forms of hominoid locomotion (brachiation, knuckle-walking or vertical climbing), it would falsify alternative hypotheses if similarities were found between the hominoid and lorisid groups. A slow-climbing arboreal quadrupedal ancestor, with enhanced joint mobility and grasping capabilities, would provide a reasonable postcranial model from which the morphology seen in extant apes, associated with more specialised locomotor patterns, could quite easily have derived (Kelley, 1997).

THESIS OUTLINE

The thesis is organised as follows: Chapter 1 is a brief outline of the purpose of study, and also includes an overview of the theories of locomotor classification and a description of the diverse locomotor behaviours observed within the order Primates. Locomotor categories are addressed with reference to the major primate divisions, although they traverse the "customary primate groupings" and are known to vary considerably between closely related genera (Ashton and Oxnard, 1964: 3). Chapter 2 introduces the early Miocene catarrhine genera relevant to the study, and provides a summary of previous analyses of the postcrania of these taxa. The final section in this chapter details the previous hypotheses that have been advocated for the locomotor behaviour of these early genera, and thus the initial locomotor adaptations of the hominoids on the whole. Chapter 3 examines previous literature about the wrist and ankle morphology in extant hominoids, lorisids, and the early Miocene forms, respectively (in a comparative context with arboreal cercopithecoids and ceboids). Chapter 4 presents the aims and objectives of this analysis. The methodology and materials used in the study are detailed in Chapter 5, and a full set of results is presented in Chapter 6. Finally, Chapter 7 serves to summarise and discuss the results achieved in the analysis.

PRIMATE LOCOMOTION: AN OVERVIEW OF CLASSIFICATION

The order Primates is characterised by a remarkable range of diversity across the spectrum of its behaviours and associated morphology. Among the most well

studied behaviours are locomotor and postural patterns, and much of the structural variation of primate postcrania may be related to these activities (Fleagle, 1999). Locomotion, which can be viewed in its simplest form as displacement movement from one place to another (Fleagle, 1980), is more diverse among primates than in any other mammalian group (Fleagle, 1999).

Throughout the history of primatology, theorists have attempted to classify patterns of locomotion within the order, by behavioural and morphological criteria, with a view to reconstructing aspects of both primate and human evolution (e.g. Erikson, 1963; Ashton and Oxnard, 1964; Napier and Napier; 1967; Aiello, 1981). The extent of diversity, however, has proven problematic for reaching any solid consensus for classification. Indeed many studies have found that most primates use a range of locomotor patterns, often context specific in terms of utility (travel/feeding), forest type, and forest level (Mittermeier and Fleagle, 1976; Mittermeier, 1978; Fleagle, 1980; Oxnard et al., 1990; Bergeson, 1998; Dagosto and Gebo, 1998). It is important, however, to attain a precise classification of primate locomotor repertoires for the purpose of comparative morphological studies, as locomotor inference of fossil species is largely dependent upon relating particular morphological features with specific locomotor capabilities in extant forms.

Primate body size ranges from 100g to 200kg (Fleagle, 1980), and the observed locomotor repertoires include leapers, climbers, brachiators, knuckle-walkers and a variety of quadrupeds, both terrestrial and arboreal (Napier and Napier, 1967; Fleagle, 1999). Many primates can be seen as essentially arboreal quadrupeds, engaging in four-limbed running and walking on top of branches (Fleagle, 1980). These species are usually characterised by fore- and hindlimbs of equal lengths [intermembral index =approx. 100] (Fleagle, 1999). The limbs also tend to be short relative to body size, or habitually flexed, which has the effect of bringing the centre of gravity closer to the arboreal support for greater balance in this precarious environment (Schmitt, 1998; Fleagle, 1999). Arboreal quadrupeds often have a long tail, which acts as an additional balancing agent (Fleagle, 1999). Some primates, however, are specialised for more hindlimb or forelimb

dominated locomotion. Vertical clinging and leaping requires an emphasis on hindlimb propulsion, and thus the hindlimbs in these species are longer than the forelimbs (intermembral index <100 [Fleagle, 1999]). Primates that incorporate forelimb suspension in their locomotor repertoires (for example, the brachiating hylobatids) tend to have relatively longer forelimbs (intermembral index >100) to reflect the greater reliance on the arms for propulsion (Zihlman, 1992; Fleagle, 1999). Additionally, some primates (e.g., *Papio*) have adapted to terrestrial living and tend to have relatively longer limbs and shorter phalanges than their arboreal counterparts, which may reflect selection for speed rather than balance (Fleagle, 1999).

Difficulties arise, however, where locomotor types are not clear-cut, and most theorists have recognised this as a weakness in their classifications (Erikson, 1963; Ashton and Oxnard, 1967; Napier and Napier, 1967). Generally, categories such as quadrupedalism are not adequate to describe the wide range of gaits found among primate genera, and they say nothing of the secondary locomotor repertoires of such animals. Many primates have a range of locomotor capabilities, and utilise more than one specific locomotor type in their repertoires, depending upon the structural context and the type of locomotion undertaken, such as travel/feeding (Fleagle, 1980). In these cases, it is sometimes difficult to recognise how morphological features relate to locomotor capabilities.

What is clear from the different classificatory models is that primate locomotion is highly varied, more so than any other mammalian order (Fleagle, 1999), and attempts to categorise depend primarily on the criteria of the analyst (Oxnard et al., 1990). The different systems of locomotor classification have, in their time, offered useful insights into primate behaviour, and Napier and Napier's (1967) model is still frequently used today as a general overview (Table 1). The questions arise, however, as to whether or not these definitions should be based on behavioural or morphological criteria and correlations between anatomical features and locomotor behaviour.

Category		Sub-type		Activity	Primate genera
1.	Vertical Clinging and Leaping			Leaping in trees and hopping on the ground.	*Avahi, Galago, Hapalemur, Lepilemur, Propithecus, Indri, Tarsius*
2.	Quadrupedalism	I.	Slow climbing type.	Cautious climbing - no leaping or branch running.	*Arctocebus, Loris, Nycticebus, Perodicticus*
		II.	Branch running and walking type.	Climbing, springing, branch running and jumping.	*Aotus, Cacajao, Callimico, Callithrix, Cebuella, Cebus, Cercopithecus, Cheirogalus, Chiropotes, Lemur, Leontideus, Phaner, Pithecia, Saguinus, Saimiri, Tupaia*
		III.	Ground running and walking type.	Climbing, ground running.	*Macaca, Mandrillus, Papio, Theropithecus, Erythrocebus*
		IV.	New World semi-brachiation type.	Arm-swinging with use of prehensile tail; little leaping.	*Alouatta, Ateles, Brachyteles, Lagothrix*
		V.	Old World semi-brachiation type.	Arm-swinging and leaping.	*Colobus, Nasalis, Presbytis, Pygathrix, Rhinopithecus, Simias*
3.	Brachiation	I.	True brachiation.	Gibbon type of brachiation.	*Hylobates, Symphalangus*
		II.	Modified brachiation.	Chimpanzee and orang-utan type of brachiation.	*Gorilla, Pan, Pongo*
4.	Bipedalism			Striding.	*Homo*

Table 1: Locomotor classification [after Napier & Napier, 1967]

All the behavioural categories used in classification can be somewhat misleading, in that the spectrum of locomotor patterns that each encompasses is so great. Important distinctions can effectively be submerged into overarching categories in classification, which can be somewhat ambiguous (Prost, 1965). The term quadrupedalism, for example, can invoke any number of diverse locomotor types, with different gaits, speeds and substrates used, and of course each subtle difference may necessitate fundamental changes in structural morphology (Fleagle, 1980; Rollinson and Martin, 1981; Cant, 1988; Walker, 1998). Similar ranges of behaviour can be encompassed within other locomotor categories: suspension, climbing and leaping (e.g. Prost, 1965). Walker (1998) suggests that broad cateogories of positional behaviour tell us little about biomechanics and body orientation during such activities, and thus terminology and classification need to be more clearly defined. In addition, these classifications give no

indication of the frequency and duration, the purpose, and/or the circumstances of locomotor behaviours (Day, 1979).

Certain morphological features are often interpreted to be functionally related to specific locomotor types, simply because some of the genera that exhibit the anatomical features utilise that form of behaviour within their repertoire. In these cases underlying basic functions can be disregarded, and little attention is paid to those taxa that exhibit the traits but not the behaviour. On the whole, correlates between morphology and behaviour must be quantitatively assessed in order to confidently interpret behaviours in fossil primates (Mittermeier, 1978; Dagosto and Gebo, 1998).

LOCOMOTOR DIVERSITY ACROSS THE MAJOR PRIMATE DIVISIONS

Lemuroidea

There are seven families of living strepsirhines, five of which exist solely on the island of Madagascar off the southeast coast of Africa: cheirogaleids, lemurids, lepilemurids (or megaladapids), indriids and daubentoniids. The other two families are found on the mainland of the Old World: lorises in Africa and Asia, and galagids in Africa (Fleagle, 1999). In addition to the present day strepsirhines, there was also a huge radiation of sub-fossil lemurs on Madagascar whose relatively recent extinction may have been initiated by the arrival of human beings and the introduction of non-native mammals (Fleagle, 1999). The strepsirhines show enormous diversity in body size, morphology, and locomotor behaviour between genera and, in some cases, species (Jungers, 1979; Fleagle, 1999). Indeed, strepsirhines are observed to engage in vertical clinging and leaping, arboreal quadrupedalism, as well as deliberate climbing and suspensory behaviours (MacLatchy, 1998).

The Malagasy forms show two types of locomotion: the cheirogaleids, lemurids and daubentoniid are primarily quadrupedal, whilst the indriids and lepilemurids are vertical clingers and leapers. These patterns, however, are by no means exclusive; some lemurs are capable of a combination of methods of travel and

nearly all are able to use a variety of postures when feeding or resting (Tattersall, 1982). Godfrey (1988) suggests that most Malagasy strepsirhines are also adept vertical climbers, utilising a combination of both horizontal and vertical supports.

The largest of the extant indriids, the tailless *Indri indri* is a highly specialised leaper, having very long propulsive hind limbs, relatively long, slender forelimbs and extremely long hands and feet. This species travels by leaping between vertical supports, usually in the lower strata of the forest where such supports are most abundant (Fleagle, 1999). *Propithecus* (sifaka) moves in a similar way and is known to travel by bipedal hopping when it occasionally comes to ground (Fleagle, 1999). Vertical climbing and bimanual suspension are also frequent forms of locomotion utilised by indriids (Gebo and Dagosto, 1988), and hindlimb postures are common during feeding (Tattersall, 1982). It is unusual to note that forelimb suspension is more common amongst the hindlimb dominated lemuroid genera than among quadrupeds (Tattersall, 1982). *Hapalemur griseus* (gentle lemur) is the most versatile of the Malagasy strepsirhines. Although typically clingers and leapers, they combine quadrupedal walking and running with leaping between both horizontal and vertical supports. Although they rarely come to ground, quadrupedal walking has been observed at this level (Tattersall, 1982; Fleagle, 1999).

In contrast to the vertical clingers and leapers, the quadrupeds have shorter hind and forelimbs, flexed during movement and rest periods for stability and balance (Tattersall, 1982). The smallest of the lemurs, *Microcebus*, occupies a 'fine branch niche' in the undergrowth and lower levels of the forest strata, typically using a fast quadrupedal locomotion, scurrying along small twigs and branches, and frequently coming to ground (Tattersall, 1982; Fleagle, 1999). The larger *Mirza coquereli* (Coquerel's dwarf lemur) and *Phaner furcifer* (fork-marked lemur), however, combine running along horizontal branches with leaping between branch tips (Tattersall, 1982; Fleagle, 1999). The lemurids are primarily quadrupedal. *Varecia variegata* (ruffed lemur) is agile and adept at both quadrupedal running along horizontal or diagonal supports and climbing vertical trunks. They also leap among the fine branches at the edge of the forest canopy and use hindlimb suspension for feeding below branches (Tattersall, 1982;

Meldrum et al., 1997; Meldrum, 1998; Fleagle, 1999). *Eulemur fulvus* and *Lemur catta* are both quadrupedal forms, but occupy different strata: the former is predominantly arboreal, utilising running and leaping, whilst *L. catta* is semi-terrestrial (Tattersall, 1982; Fleagle, 1999). Of the quadrupedal lemurs, *Daubentonia madagascariensis*, or the aye-aye, is the slow climber, travelling along both vertical and horizontal supports, occasionally quadrumanously beneath the branches, and frequently descending to ground (Tattersall, 1982; Fleagle, 1999).

There seems to be a clear relationship between body size, vertical habitat and locomotor pattern: the larger species are restricted by body weight to more substantial supports higher up, whilst the smaller *Microcebus* is able to utilise tiny twigs and branches in the undergrowth (Tattersall, 1982). In addition, vertical clingers and leapers travel in the lower to intermediate strata, where vertical supports are less obscured by continuous vegetation. These species tend to be relatively small, and this type of locomotion was probably an adaptation for smaller species, enabling them to travel continuously through lower levels of the forest without having to descend to ground. The larger quadrupedal species, however, are able to bridge across gaps between branch ends, and tend to inhabit the higher levels where they can move among the continuous forest canopy (Tattersall, 1982).

The sub-fossil Malagasy strepsirhines include species of indriids, lemurids, lepilemurids and daubentoniids (Fleagle, 1999). These taxa were quite different from their modern counterparts: large bodied (*Archaeoindris* has been estimated to have been the size of a male gorilla) and probably diurnal (Fleagle, 1999). Postcranial remains showing long forelimbs (relative to hind limbs) and long curved phalanges, suggest that some species (e.g. *Palaeopropithecus*) were adapted to suspensory locomotion, possibly quadrumanous climbing beneath horizontal supports, whilst others (e.g. *Archaeolemur*) were primarily adapted to terrestrial lifestyles (Godfrey, 1988; Fleagle, 1999; Hamrick et al., 2000). The unusual *Megaladapis*, a species with similarities to the modern lepilemur, showed locomotor behaviour similar to the Australian koala, clinging and climbing on vertical supports (Godfrey, 1988; Fleagle, 1999; Hamrick et al., 2000). Godfrey

(1988) proposed that climbing and slow quadrupedalism might have been important elements of the positional behaviour of many of the extinct lemurs, including *Palaeopropithecus*, *Archaeoindris*, *Mesopropithecus*, and *Megladapis*.

Lorisoidea

In comparison with the Malagasy strepsirhines, lorises and galagids are much less diverse in their adaptations, probably due to the greater competition with other primates and mammals. The family Lorisidae includes species from Africa and Asia: the potto (*Perodicticus potto*), the golden potto (*Arctocebus calabarensis*), the slender loris (*Loris tardigradus*) and the slow loris (*Nycticebus coucang*). All the lorisids are small, arboreal and solitary nocturnal foragers (Fleagle, 1999). The lorises are characterised by their slow, stealthy quadrupedal climbing, on a variety of arboreal supports (Walker, 1969; Jungers, 1979; Dykyj, 1980; Runestad, 1997) and minor locomotor differences can be attributed to different supports used rather than differences in their positional repertoires (Jungers, 1979). They all possess elongated limbs, of similar lengths, flexible joints specialised for 'bridging' across gaps between branches, and robust hands and feet with strong grasping capabilities in a wide variety of positions (Walker, 1969; Cartmill and Milton, 1977; Grand, 1967). In all species, the tail is either short (*P. potto*) or absent. Although subtle differences in locomotion have been noted between the loris species, the basic pattern is the same. Locomotion usually proceeds with three extremities grasping the support any one time, with the hands and feet laterally deviated in dorsiflexed wrist and ankle positions (Walker, 1969; Cartmill and Milton, 1977; Grand, 1967). Below-branch quadrupedalism has also been noted in these species (Ashton and Oxnard, 1964; Cartmill and Milton, 1977; Maclatchy, 1998) although Walker (1969) observes that this is primarily when moving from vertical to horizontal supports, rather than in habitual progression. Locomotion has also been observed on the ground, where the locomotor pattern is the same.

Galagids are primarily agile vertical clingers and leapers with hugely elongated hindlimbs, although some species, for example *Otolemur crassicaudatus* (thick-tailed bushbaby), combine this with quadrupedal running and walking (Fleagle,

1999). All species leap between vertical supports in a frog-like fashion, using their hindlimbs as the initial propulsion, and *Euoticus* can travel up to 40 feet in a single leap (Napier and Walker, 1987). All species utilise a bipedal hopping gait, in combination with quadrupedalism, on the ground (Oxnard et al., 1990; MacLatchy, 1998).

Ceboidea

As with the strepsirrhines, the platyrrhines are diverse in terms of both their locomotor repertoires and their associated morphology. All, however, fall within a relatively conservative 70 to 100 range in their intermembral indices (Fleagle, 1999). Many subfamilies may be identified within the grouping, although only six are recognised here: Callitrichinae, Cebinae, Aotinae, Callicebinae, Pitheciinae and Atelinae (after Fleagle, 1999). The callitrichines are the smallest of these primates and include the marmosets, tamarins and Goeldi's monkey. All species within this subfamily are arboreal quadrupeds (walking and running) and some are adept leapers (Fleagle, 1999). In addition, some species (e.g.*Callimico goeldii*) habitually cling to, and leap between, vertical supports (Fleagle, 1999).

Aotus (owl monkey), the single genus in the aotine subfamily, is for the most part quadrupedal, but is also an adept leaper (Fleagle, 1999). The callicebines are similar morphologically to the aotines, and are also quadrupedal. *Callicebus* does, however, show variation in the frequency of leaping between species, and similar variation in vertical clinging habits (Fleagle, 1999).

The pitheciines are an extraordinary grouping of three genera: *Pithecia*, *Chiropotes* and *Cacajao*. Within this group the locomotion of the genera varies hugely. *Pithecia* is the most saltatory of the New World monkeys, spending approximately 75% of moving time using this form of locomotion, whilst *Cacajao* and *Chiropotes* are primarily arboreal quadrupeds, frequently using hindlimb suspension (Walker and Ayres, 1996; Meldrum, 1998; Walker, 1998; Fleagle, 1999)[1]. Walker (1998) suggests that this high percentage of leaping in *Pithecia* is

[1] Walker (1998) suggests that *Pithecia* utilises leaping during about 40% of locomotor bouts, compared to *Chiropotes* leaping for only 25%.

reflected in its essentially prosimian-like postcrania, whilst *Chiropotes* does not exhibit these morphological specialisations.

The cebines, *Cebus* and *Saimiri,* are both primarily arboreal quadrupeds but the two genera combine this form of locomotion with other specialisations. *Cebus* utilises its prehensile tail for additional support, whilst *Saimiri* is a much more versatile leaper (Fleagle, 1999).

The New World subfamily Atelinae (*Alouatta*, *Ateles*, *Brachyteles*, and *Lagothrix*) is characterised by a large prehensile tail (Meldrum, 1998)[2] and suspensory postural and locomotor repertoire. Erikson (1963) classified these species as brachiators. Ashton and Oxnard (1964) defined *Alouatta* as a slow quadruped aided by its prehensile tail that frequently used leaping and bridging to cross between trees in its arboreal environment. The remaining three genera, however, were classified as essentially quadrupedal walkers and runners, habitually using arm-swinging and their prehensile tails to aid climbing and in locomotion. Napier and Napier (1967) described the atelines as quadrupeds of the New World semi-brachiation sub-type. This latter model has been particularly criticised with reference to the 'semi-brachiator' subtype, which was deemed inadequate on two counts: that the group defined no single locomotor pattern, and that locomotor diversity was greater than similarities within the category (Mittermeier & Fleagle, 1976). Cant (1986) states that Napier and Napier's semi-brachiating classification obscures important differences between the organism's postcrania and its use of its natural habitat. Ankel-Simons (1983) proposes that in the case of this 'semi-brachiation' category, group cohesion is morphological in origin, rather than behavioural. Indeed, observational studies of ateline genera have shown a wide locomotor diversity within the group, with differences in both modes of locomotion used and time spent utilising each locomotor pattern (Grand, 1968; Richard, 1970; Mendel, 1976; Mittermeier, 1978; Fleagle & Mittermeier, 1980; Cant, 1986; Youlatos, 1996; Bergeson, 1998; Defler, 1999).

---

[2] The ateline prehensile tail can comprise up to 8% of body weight, which illustrates its importance in the positional behaviours of these taxa (Zihlman, 1992).

The atelines, however, do show elements of suspensory locomotor and postural behaviour that is unparalleled within the Old World monkeys. Indeed, their repertoires can be most closely related to that of the lesser apes, in their tendency towards under-branch suspensory behaviour. Cant et al. (2001) suggest that whilst none of the cercopithecoids show intermediary adaptation towards suspensory behaviour, the atelines do, which implies that the cercopithecoids are quite derived from the primitive catarrhine morphology. In view of their inclination towards suspensory positional behaviour, the atelines have been proposed as good examples for the analysis of the evolution of the specialised behaviours of extant apes (see also Erikson, 1963) and some studies have noted parallels between the morphology of Miocene fossil primate postcrania and these extant below-branch feeding primates (e.g., Aiello, 1981; Feldesman, 1982; Rose, 1996). *Alouatta* has also been advocated as an ideal model to represent the basal anthropoid morphotype in terms of postcranial adaptations and locomotor behaviour (Schon Ybarra and Conroy, 1978). It has been suggested that this group may provide useful insights into the evolution of suspensory behaviour in the Hominoidea. Thus, this group has often been used as a model with which to compare early hominoid postcrania, in an attempt to establish the evolution of this element of behaviour in extant apes (e.g. Rose, 1996).

Cercopithecoidea

The cercopithecoids are relatively uniform in both their postcrania and locomotor behaviour (Rollinson and Martin, 1981) and can be divided into two subfamilies, cercopithecines and colobines. The Old World monkeys as a group, however, are quite derived in their locomotor adaptations (Strasser, 1988). These taxa all fall within a relatively conservative 1-30kg in body weight (Rollinson and Martin, 1981) and most genera are predominantly quadrupedal, with some more terrestrially adapted. Within the broad arboreal quadruped category, however, some species are inclined towards more saltatory locomotion while others are known to be more reliant on climbing and suspension (Fleagle, 1980; Rollinson and Martin, 1981; Fleagle, 1999; Gebo and Chapman, 2000). In general, the cercopithecines have equal length limbs, whilst the colobines have relatively longer hindlimbs, which is reflective of their differing locomotor tendancies

(Fleagle, 1999). In a study of the behaviours of Malayan macaques (*Macaca fascicularis* and *M. nemestrina*) and leaf monkeys (*Presbytis melalophos* and *P. obscura*), Fleagle (1980) found that all species were fundamentally quadrupedal, but each combine this basic pattern with other behaviours. Both of the leaf monkeys utilise leaping behaviours and vertical climbing, although they engage in vertical quadrupedal walking rather than the quadrumanal climbing seen in apes. Both species use quadrupedalism during feeding bouts, but *P. melalophos* tend to leap more in travel. Of the macaque species, *M. fascicularis* is predominantly arboreal, combining quadrupedal walking and running behaviours with climbing and leaping[3], whilst *M. nemestrina* is more terrestrially inclined and less skilful at climbing and leaping (Fleagle, 1980).

Gebo and Chapman (2000) studied five sympatric African species: *Cercopithecus ascanius*, *C. mitis*, *Lophocebus albigena*, *Colobus badius* and *C. guereza*. Again, all were found to be predominantly arboreal quadrupeds, but they differed in the combinations of their locomotor activities. *Cercopithecus ascanius* undertakes frequent climbing, but neither of the *Cercopithecus* species engage in quadrupedal suspension, bridging, bimanualism, bipedalism or vertical bounding. *L. albigena* and both *Colobus* species combine quadrupedalism with frequent leaping. Within *Colobus*, *C. badius* is more inclined toward climbing, whilst *C. guereza* leaps more frequently. This study found that body-size differences could not account sufficiently for locomotor differences, although the smaller species engage in more climbing whilst the larger tend to leap, which is the reverse situation to that found in platyrrhine species (Gebo and Chapman, 2000; Fleagle and Mittermeier, 1980). Additionally, the authors observed *Colobus badius* over several seasons and found that locomotor frequency showed seasonal variability (Gebo and Chapman, 2000).

Whilst primates have an anatomical design and body dimensions that affect their movement possibilities, most species are ecologically flexible in their use of positional behaviour. Consequently, more attention needs to be committed to the

---

[3] Cant (1988) reported this species to engage in vertical climbing, and pronograde and vertical clambering, which he proposes as a reasonable model for an early stage of hominoid evolution before true orthogrady.

understanding of intraspecific variation in extant species, particularly with reference to the relationship between behaviour, ecology and anatomy, in order to apply this knowledge for a better understanding of fossil primates (Gebo and Chapman, 2000).

Hominoidea

The living hominoids vary considerably in their body size, from approximately 5kg in *Hylobates*, to up to 200kg in male gorillas (Jungers, 1988). Superfamily Hominoidea is perhaps the most contentious of the primate groups in terms of locomotion. It has long been the trend to classify these genera within a 'brachiating' locomotor category (e.g.Napier and Napier, 1967; Erikson, 1963;Ashton and Oxnard, 1964), despite the fact that only the hylobatids habitually undertake this form of locomotion. Indeed, brachiation is rarely observed in the great apes[4] (Fleagle et al., 1981). Kelley (1997: 175) states "brachiation is a much abused and often ill-defined term, embodying different sets of behaviour for different workers". This is, perhaps, an issue of semantics, rather than one of classification. Often, suspensory locomotor behaviour has been defined under an all-encompassing brachiation category, which has the effect of obscuring individual locomotor differences between suspensory species (Fleagle et al., 1981; Kelley, 1997). Hominoids as a group, however, use a wide range of locomotor behaviours including quadrupedalism, bipedalism, quadrumanous climbing, brachiation and leaping (Tuttle, 1986; Jungers, 1988; Sarmiento, 1994).

Hylobatids are renowned for their rapid arm-over-arm ricochetal locomotion, which is used here as the traditional definition of brachiation (e.g., Napier, 1963; Andrews and Groves, 1976; Fleagle, 1980). Fleagle (1980) noted four categories of locomotion among hylobatids, which varied in frequency between species: quadrumanal climbing, brachiation, bipedalism and leaping. In most species, brachiation is the most frequent form of locomotion during travel, whilst climbing is most commonly undertaken during feeding. There are also differences between gibbons and siamangs, which might be attributed to body size differences: the

[4] It is important to note that whilst the author acknowledges humans to be part of a great ape grouping, references to the 'great apes' in this study refer only to *Pongo*, *Gorilla* and *Pan*.

smaller gibbon is more adept at ricochetal arm-swinging, whilst the larger siamang tends to climb more frequently (Fleagle, 1980; see also Tuttle, 1986). Locomotor type is also highly dependent on support use. Climbing is more viable on small supports, for weight distribution over multiple supports in variable positions, whereas brachiation is utilised between larger supports (Fleagle, 1980).

Pongo, whilst fundamentally suspensory when in an arboreal environment, is characterised by a slower, more versatile quadrumanous form of climbing locomotion. Its repertoire includes: climbing/clambering, bridging and transferring, vertical ascents and descents[5], hoisting, pedal assisted arm-swinging, quadrupedal suspension below branches and tree-swaying (Napier, 1963; Tuttle, 1986; Gebo, 1996). Tuttle (1986: 40) suggests that orangutan suspension "lacks the speed and flow of the specialised ricochetal brachiation of gibbons and siamangs". Adult males spend a considerable amount of time on the ground, unlike females, which might be attributed to their larger body size (Tuttle, 1986; Gebo, 1996), and during arboreal locomotion males utilise more branch swaying, whilst females engage in quadrumanous clambering (Zihlman, 1992). The orangutan is very unusual as a mammal of very large body size engaging in significant arboreal activity, and this might be attributed to their preference for swamp forest habitats, where the forest floor is flooded for long periods (Tuttle, 1969).

The African apes are generally far more terrestrial in their locomotor behaviour than the Asian species, and use a characteristic knuckle-walking form of quadrupedalism, where the main body weight is supported on the dorsal surface of the third and fourth digits of the flexed hand (Tuttle, 1967; Fleagle, 1999). The majority of the arboreal climbing component in their locomotor repertoires, however, is practised on vertical supports, as in *Pongo* (Gebo, 1996).

Chimpanzees are more arboreal than gorillas, and are adept vertical climbers. Sub-adults spend more time in trees than mature individuals, and move more easily in this environment. Adults become increasingly cautious in an arboreal context,

---

[5] Gebo (1996) reports that in *Pongo*, 61% of arboreal travel is spent utilising vertical support.

perhaps due to their body size (Tuttle, 1986). Reports differ concerning the frequencies of brachiation, jumping and leaping, and bridging behaviours, although this may well be due to intraspecific variation caused by environmental differences (Tuttle, 1986). Chimpanzees also undertake bipedal walking for short distances on the ground (Tuttle, 1986).

The bonobo (*Pan paniscus*) is generally more arboreal in its locomotor behaviour than *Pan troglodytes* (Gebo, 1996), but also spends a considerable time on the ground using quadrupedal knuckle-walking, and occasional bipedalism. Arboreal behaviours include: arm-swinging, quadrumanous climbing, scrambling and transferring, and above-branch quadrupedalism, in either knuckle-walking or palmigrade hand postures depending on support size (Tuttle, 1986).

The gorilla is predominantly terrestrial, spending between 80 and 97% of the time at this level (Tuttle, 1986). Most arboreal activity in adults is for feeding, and individuals tend to spend most of their time near the trunk and on large vertical boughs (Tuttle, 1986). Ricochetal arm-swinging is never observed, and forelimb suspension is rare (Fleagle et al., 1981). Most arboreal activity is quadrupedal climbing (Gebo, 1996).

CHAPTER 2

Locomotor adaptations in the early Miocene hominoids

THE EARLY MIOCENE HOMINOIDS: INTRODUCTION

The earliest identified hominoid remains are dated to the beginning of the Miocene epoch, the period between 23.7 and 5.3 million years ago (Rae, 1993). The temperature at the early Miocene (23.7 – 16 mya) was much warmer than the preceding Oligocene epoch, despite fluctuating temperatures, and Africa was becoming gradually more arid (Fleagle, 1999). This particular time period was characterised by an enormous array of fossil hominoids, in terms of both diversity and abundance (Ward et al., 1997; Fleagle, 1999). Hominoid fossils are geographically restricted during the early parts of this time period to Kenya and Uganda in East Africa. During the middle and latter parts of the Miocene, however, hominoids became prolific in both Europe and Asia.

The primitive hominoids of the early Miocene were first recognised by Hopwood (1933)[6], and are now acknowledged to include four species of *Proconsul* (*P. africanus*, *P. heseloni*, *P. nyanzae* and *P. major*), *Afropithecus turkanensis*, *Afropithecus leakeyi*, *Turkanapithecus kalakolensis*, *Rangwapithecus gordoni*, *Limnopithecus legetet* and *Limnopithecus evansi*, *Dendropithecus macinnesi*, *Simiolus enjiessi*, *Simiolus leakeyorum*, *Micropithecus clarki*, *Kalepithecus songhorensis* and *Morotopithecus bishopi* (described by Hopwood [1933]; MacInnes [1943]; Le Gros Clark and Leakey [1951]; Andrews, [1974, 1978]; Fleagle and Simons [1978]; Leakey and Leakey [1986a-b, 1987]; Walker et al. [1993]; Gebo et al. [1997]). These species derive from a cluster of localities in sub-Saharan Africa, most of which are associated with volcanic centres within the Great Rift Valley (Rae, 1993). The Kenyan sites that have yielded remains include

[6] Hopwood (1933) first identified *P. africanus*, which was among the first named of the Miocene primates, found within a sample of fossils from the Koru locality in Kenya and dated to the Lower Miocene. Hopwood suggested that the new species approximated in size to *Pan*, and based on its dentition, although primitive in comparison to modern apes, he promoted it as ancestral to the chimpanzee. More recently, much of the *P. africanus* material has been reassigned to *P. heseloni* (Walker et al., 1993; Walker, 1997, Pilbeam, 1997).

Rusinga Island, Songhor, Legetet, Chamtwara, Meswa Bridge, Koru, Mteitei Valley, Karungu, Mfangano Island, Buluk, and Kalodirr. The Ugandan specimens were recovered at Napak and Moroto (Rae, 1993).

The early Miocene sites were mainly forested locations, incorporating a variety of different habitats within this broad category (Langdon, 1985). The early *Proconsul* sites at Songhor and Koru were characterised by tropical rainforested, whilst the later Rusinga island sites were probably open deciduaous forests (Andrews et al., 1997) The fauna suggests, therefore, that arboreal behaviour was an important adaptation for the early Miocene hominoids (Langdon, 1985).

Species	Epoch	Location	Estimated mass (g)
Family PROCONSULIDAE			
Proconsul	Early Miocene	Africa	
P. africanus			27, 400
P. heseloni			17, 000
P. nyanzae			28, 000
P. major			50, 000
Rangwapithecus	Early Miocene	Africa	
R. gordoni			15, 000
Limnopithecus	Early Miocene	Africa	
L. legetet			5, 000
L. evansi			6, 000
Dendropithecus	Early Miocene	Africa	
D. macinnesi			9, 000
Simiolus	Early to middle Miocene	Africa	
S. enjiessi			7, 000
S. leakeyorum			
Micropithecus	Early Miocene	Africa	
M. clarki			3, 000
Kalepithecus	Early Miocene	Africa	
K. songhorensis			5, 000
Family *Incertae sedis*			
Afropithecus	Early to? middle Miocene	Africa, Saudi Arabia	
A. turkanensis			50, 000
A. leakeyi			
Morotopithecus	Early Miocene	Africa	
M. bishopi			40, 000
Turkanapithecus	Early Miocene	Africa	
T. kalakolensis			10, 000

Table 2:Early Miocene hominoids [after Fleagle, 1999]

The early Miocene genera exhibit a large range of body size, from the 3.5kg *Micropithecus* to the 50kg *Proconsul major* and *Afropithecus* (Fleagle, 1999; Table 2). Postcrania, however, are only known for a few of the genera, and, unfortunately, much of this is fragmentary. Examination of the postcrania of these Miocene forms has revealed morphology unlike that seen in the modern genera. Locomotor repertoires were, contrary to predictions, very different from the more suspensory modes of extant hominoids, and indeed the first evidence of an emerging forelimb dominated locomotion was not apparent until the later Miocene (Ward, 1998). Perhaps the most unifying of locomotor behaviours among these early forms was that of powerful quadrupedal climbing, which appears to have been integral to the locomotor repertoires of all of the earliest apes.

PREVIOUS ANALYSES OF EARLY MIOCENE HOMINOID POSTCRANIA

The early Miocene hominoids, most particularly *Proconsul*, have been rigorously studied with respect to their postcranial locomotor skeleton, yielding a number of different interpretations (e.g. Napier and Davis, 1959; Fleagle, 1983, 1986; McHenry and Corruccini, 1983; Lewis, 1971a, 1972a-b, 1974; Rose, 1983, 1992, 1996, 1997; Walker & Pickford, 1983; Langdon, 1985, 1986; Leakey et al., 1988a-b; Ward, 1993, 1997, 1998; Begun et al., 1994; MacLatchy & Bossert, 1996). Due to the derived nature of the postcrania of extant hominoids toward forelimb dominated locomotion, early analysts expected to find similar adaptations in basal species. The assumption was that the hominoid lineage initially diverged into a below-branch niche, and was characterised by associated changes in postcrania. Many studies (e.g. Harrison, 1982, 1987; Ward, 1993a-b, 1997, 1998; Sanders and Bodenbender, 1993), however, have found that the postcrania of early hominoids are more similar, in many respects, to those of extant arboreal, quadrupedal cercopithecoids than their extant ape counterparts, although the features found in the primitive genera differ in combination to those found in any living primate[7]. The different views that have derived from the many

[7] This has somewhat hampered the reconstruction of the behaviour of these fossil primates, as comparative analyses can only be done with extant forms, and since no living primate bears the

analyses have depended largely upon the characters studied, as these early hominoids exhibit a mosaic of monkey-like, ape-like and unique features (Langdon, 1986). Much depends upon the school of thought of the author: the significance attached to a 'brachiation' model of hominoid origins (and probably also the other major hypotheses, for example knuckle-walking), and the various interpretations as to the best extant representatives (brachiators/suspensory, primitive arboreal quadrupeds, generalised climbers or more specific hominoid types) (Langdon, 1986).

This literature overview will focus on the main genera of the time period, for which postcranial material has been recovered: *Proconsul*, *Dendropithecus*, *Rangwapithecus*, *Limnopithecus*, *Kalepithecus*, *Simiolus*, *Micropithecus*, *Afropithecus*, *Turkanapithecus* and *Morotopithecus*.

One of the earliest dated of the Miocene genera is *Proconsul*. Postcranial remains are known for four species (*P. nyanzae*, *P. heseloni*, *P. africanus* and *P. major*) and *Proconsul* is perhaps the best represented, and thus most studied, of fossil hominoids from this time period (MacLatchy & Bossert, 1996). Another early Miocene hominoid, *Afropithecus*, is generally regarded to be similar to *Proconsul* in its postcrania (Leakey et al., 1988b; Rose, 1992; 1997; Andrews et al., 1997; Ward, 1997, 1998), and hence locomotor inferences for *Proconsul* have been equally be applied to this genus[8]. *Afropithecus* probably most resembled *P. nyanzae* due to similarities of body size (Leakey et al., 1988b; Leakey and Walker, 1997).

---

exact morphological features of the fossil forms, locomotor and postural inference must be tentative.

[8]The difficulties with this assumption were highlighted by Sanders and Bodenbender (1993) in their analysis of the Moroto lumbar vertebra specimen (UP 67-28). Although the specimen showed no overall similarities to any extant catarrhine, it is the earliest specimen that shows affinities to modern hominoids. If this specimen had been confidently assigned to *Afropithecus* (as the authors recommended), it would have called into question the assumed similarities in positional behaviour between *Afropithecus* and *Proconsul*. This specimen was originally assigned to *P. major*, which would have opened a similar debate about the assumed postcranial, and thus positional, similarities within *Proconsul*. It is now generally agreed that this specimen represents a unique genus, *Morotopithecus* (MacLatchy et al., 2000), but the previous literature regarding this specimen highlights the dangers of assuming overall postcranial similarity from incomplete fossil postcrania, and caution should be taken due to the mosaic nature of evolution (see also MacLatchy and Bossert [1996] in their study of the shoulder and hip of *Proconsul* and *Afropithecus*).

Proconsul species varied in body size from approximately 11kg for *P. africanus* to almost three times as much for the larger *P. nyanzae*, but despite size differences, the species show no apparent differences in overall morphology or shape (Walker & Pickford, 1983). In limb proportions, *Proconsul* was generally monkey-like, with an intermembral index estimated to 86.9[9], equivalent to that of quadrupedal monkeys, and a brachial index closest to *Pan*[10]. Overall, *Proconsul* limbs were relatively short and anatomically robust for their body size, with relatively large articular surfaces (Walker & Pickford, 1983). The most likely form of locomotion undertaken by *Afropithecus* and *Proconsul* was slow-moving arboreal quadrupedalism (Leakey et al., 1988b). *Afropithecus* and *Proconsul* are assumed to share a postcranial morphology close to that of the primitive hominoid condition (Ward, 1998), which suggests that their locomotion may be a good representative for that of the ancestral hominoid.

Analyses of the *Proconsul* forelimb have yielded differing results as to their modern affinities across various characteristics. The shoulders of *P. nyanzae* and *P. africanus* exhibit characteristics of the scapula and proximal humerus indicative of considerable mobility including overhead forelimb positions: fairly oblique scapula spine, cranially directed glenoid fossa, laterally extended acromion, greater degree of medial torsion in the humeral head, expansion of the humeral head, lateral migration of the lesser tuberosity and reduction of both the lesser and greater tuberosities in comparison to earlier catarrhine species (Rose, 1983, 1989; Walker and Pickford, 1983; Gebo et al., 1988).

In contrast, other examinations of the humerus and glenohumeral joint of *Proconsul* (e.g. Ward, 1997; Larson, 1996) have found features consistent with quadrupedal pronogrady: retroflexion in the humeral shaft and ventrally directed humeral head. These features would be compatible with a laterally placed scapula, set in a parasagittal plane on the side of the thoracic cage, as seen in quadrupedal monkeys (Ward, 1997). The degree of humeral torsion noted for *Proconsul*

---

[9] Fleagle (1999) reports the intermembral index to be 89 in *Proconsul heseloni*.
[10] Rose (1988) estimated brachial index to be 96.

seemingly exceeds that of cercopithecoids, but is not as extensive as in extant apes, which would concur with the earlier observations.

Studies of the humero-radial joint of *P. africanus* suggest that the *Proconsul* forelimb was capable of considerable flexion-extension, with a high degree of mediolateral stability throughout the range of movement, and a reasonably high range of supination/pronation (comparable to extant cebids)[11]. The elbow joint is thought to be most similar to that of extant hominoids, (Rose, 1983; see also Rose, 1988, 1992; 1997; Walker and Pickford, 1983). Features of muscular insertion and the posterior direction of the olecranon process, also suggest a degree of terrestriality in the larger *Proconsul* species (Rose, 1983; Fleagle, 1983).

Studies considering the wrist and hand of *Proconsul*, have reached varying conclusions: some equating the morphology with hominoids (Lewis, 1971a, 1972a-b, 1974) and other suggesting it to be more monkey-like (Napier and Davis, 1959; Schon amd Ziemer, 1973; Morbeck, 1975; Corruccini et al., 1976; Fleagle, 1983; McHenry and Corruccini, 1983; Rose, 1983; Harrison, 1987). There is no evidence to suggest that these species were adapted to knuckle walking (McHenry and Corruccini, 1983) and most studies have agreed that *Proconsul* possessed powerful grasping capabilities in the hand (Rose, 1983, 1992, 1996, 1997; Begun et al., 1994).

With respect to the hindlimb in *Proconsul*, a mosaic of features is again evident. The hip joint is capable of a wide range of mobility, indicated by the low greater trochanter, high femoral neck and spherical femoral head (Fleagle, 1983; MacLatchy & Bossert, 1996), and the femoral head shows similarities to arboreal colobines (Ward, 1997)[12]. The knee joint, on the other hand, is more similar to living hominoids and cebids, with flexibility of posture and adaptation to heavy loading (Ward, 1997). The morphology of the *Proconsul* patella is similar to

---

[11] These findings are contested by Harrison (1987), who suggests that *Proconsul* lacked the specialisations of the elbow consistent with increased potential for extension and rotation of the forelimb, as well as lacking adaptations towards increased mobility in the wrist, ankle, hip and knee joints.

[12] Ruff et al. (1989) suggest that *Proconsul* femora fall into two distinct categories: the smaller *P. africanus* specimens are most similar to cercopithecines in their size and proportions, whilst the larger *P. nyanzae* are more like *Pan paniscus*.

extant hominoids, and probably represents a primitive hominoid condition ill adapted to running or leaping (Ward et al., 1995).

Analyses of the ankle and foot of *Proconsul* have generally agreed upon a high degree of mobility within the mid-tarsus, with a powerfully robust and divergent hallux (Fleagle, 1983; Begun et al., 1994; Ward, 1997). The robusticity of both the fibula and hallux are also suggestive of strong grasping and climbing capabilities (Fleagle, 1983; Walker and Pickford, 1983; Ward, 1997).

The morphology of the hand and foot phalanges suggests that the hands and feet of *Proconsul* are very similar, capable of both powerful manual and pedal grasping (Rose, 1992; Begun et al., 1994). Although these specimens share derived characteristics with modern apes, they lack the longitudinal curvature seen in the more suspensory primates (Begun et al., 1994). Overall, the hands and feet of these species are indicative of adaptation to slow vertical and sub-vertical climbing, and the features suggest grasping rather than palmigrade quadrupedalism (Begun et al., 1994).

Overall, the appendicular skeleton of *Proconsul* (and by default *Afropithecus*) has been found to be considerably more primitive than that of modern hominoids, in many aspects adapted primarily for arboreal quadrupedalism (for example, relatively short forearm, features of the proximal humerus and an unreduced thumb). The limbs were robust overall, more like modern cercopithecoids, *Pan* and non ateline ceboids than *Hylobates* and atelines (Ruff et al., 1989). Analysts generally agree, however, that the quadrupedal gait of *Proconsul* was probably one of slow, deliberate progression, rather than the agile running and bounding behaviours of arboreal monkeys (e.g. Kelley and Pilbeam, 1986).

Proconsul and *Afropithecus* may have differed fundamentally in their ranges of mobility at the shoulder and hip joints (MacLatchy and Bossert, 1996). *Proconsul* shows restricted mobility in the shoulder, but a very mobile hip, whilst *Afropithecus* has a shoulder and trunk more compatible with orthograde and suspensory postures, but only a moderately mobile hip (MacLatchy and Bossert,

1996). This mobility of the limbs is probably related to suspension, but is different to all extant anthropoids that exhibit patterns where both shoulder and hip are either mobile or not. In effect, therefore, these relationships are effectively 'de-coupled' in these early species, which illustrates the mosaic nature of early hominoid postcranial evolution (MacLatchy and Bossert, 1996). These findings might support a model where both genera were fairly generalised arboreal quadrupeds, utilising deliberate climbing, and supplementing these behaviours with either hindlimb (*Proconsul*) or forelimb (*Afropithecus*) suspension.

Most studies have indicated, however, that *Proconsul* was probably capable of a greater range of mobility within the limbs at all joints (seen most particularly in the distal humerus and elbow joint) than extant cercopithecoids, thus suggesting more variable locomotor and positional repertoires within an arboreal environment (Fleagle, 1983; Rose, 1983, 1989; Walker and Pickford, 1983; Kelley and Pilbeam, 1986; Gebo et al., 1988; MacLatchy & Bossert, 1996). This mosaic of primitive and derived features, however, would accord with any expectations of a basal member of the Hominoidea.

The relative shape and length of the torso of *P. nyanzae* (based on specimen KNM-MW 13142 vertebrae and hip bone) falls well within the range for arboreal, quadrupedal monkeys indicated by a long vertebral column, long torso cranio-caudally, transversely narrow and dorso-ventrally deep thoracic cage, and powerful spinal musculature (Ward, 1993a-b; Ward et al., 1993). The almost complete hip bone of *P. nyanzae* is most reminiscent of pronograde arboreal quadrupeds, and shows no evidence of orthograde postures (Ward et al., 1993). These features are compatible with extensive flexion of the spine, implying pronograde, quadrupedal locomotion. Whilst *Proconsul* retains features of cercopithecoid-like dorsoventral flexion in the lower back, the evidence suggests that this is not to the same degree as extant monkeys (Sanders and Bodenbender, 1993). Indeed, the characters of the *Proconsul* vertebrae, including the inferred musculature, indicate that these species were less capable of the leaping, bounding

and running behaviour characteristic of many extant cercopithecoids (Sanders and Bodenbender, 1993).

Analysis of the sacral vertebrae in *P. africanus* has, however, provided evidence that this species did not have a tail (Ward et al., 1991). "The lack of tail in *Proconsul* suggests that tail loss in hominoids was not a consequence of forelimb dominated locomotor patterns. Rather, tail loss preceded these locomotor changes in the hominoid lineage" (Ward et al., 1995: 219). The reason for tail loss in this arboreal species remains unexplained, although some authorities have attributed this as an adaptation to orthogrady (e.g. Begun et al., 1994). It is reasonable to assume, however, that tail loss was integral to the evolution of hominoid specialisations. Kelley (1997) suggests that *Proconsul* developed powerful grasping hands and feet to compensate for its lack of tail and large body size in an arboreal environment. Increased limb mobility would be necessary in balance whilst grasping. Rose (1996: 11) appears to agree with this conclusion, " it is possible that initially, derived hominoid features represented functional complexes that allowed relatively large-bodied but tail-less animals to manoeuvre successfully in an arboreal environment"

Proconsul seemed to possess a mosaic of extant Old World monkey, New World monkey and ape features (Walker & Pickford, 1983), and probably had a quite varied positional repertoire incorporating a large element of slow climbing (Rose, 1983; Walker and Pickford, 1983; Walker, 1997). This apparent slow, quadrupedal, climbing behaviour has been equated to that of the less agile New World atelines (Aiello, 1981; Rose, 1996). Overall, the plethora of evidence suggests that *Proconsul* was a powerful, arboreal quadruped, with joint mobility that allowed an extensive range of movement in all four limbs, whilst retaining a more monkey-like bauplan of the axial skeleton. Its strong, grasping pedal and manual capabilities are indicative of adaptation to scansorial locomotion, which would equate with the increased limb mobility (Begun et al., 1994; Rose, 1997).

Postcrania for the other early Miocene African hominoids are less prolific, and thus locomotor inferences are much more speculative. *Rangwapithecus* was very similar to *Proconsul* in its hindlimbs, but with more derived hominoid features in

the ankle region, although Ward (1997: 107) suggests that this "may closely reflect individual variation rather than taxon-specific functional patterns". Few postcranial remains are known for *Limnopithecus*, and the isolated specimens indicate that the locomotor and positional capabilities of this genus may have been virtually identical to *Proconsul* (Langdon, 1986).

Turkanapithecus is estimated to be similar in body size to the larger cebids (10kg) and shows many similarities to *Proconsul*, but with several distinctive features (Leakey et al., 1988a). Overall, the same general combination of cercopithecoid, hominoid, and unique characteristics is evident. More recent studies, however, have suggested that elements of the forearm morphology in this species indicate a greater degree of vertical climbing and hoisting than in *Proconsul* and *Afropithecus*, with a combination of uniquely derived features and shared derived characteristics with extant hominoids (Rose, 1996; Ward, 1997). The *Turkanapithecus* ulnae, however, (as those of *Proconsul*) reflect a functional anatomy consistent with considerable climbing and habitual arboreal, quadrupedal behaviours (Richmond et al., 1998). The femur is more robust than in *Proconsul*, and has been equated with that of *Alouatta* (Rose, 1996; Ward, 1997). Whilst there is no evidence for hindlimb suspension in *Turkanapithecus*, from its similarity to *Alouatta* it might be inferred that this was part of its positional repertoire (Rose, 1996).

Dendropithecus macinnesi, with its long, slender limbs, is proposed as the most suspensory of the early Miocene hominoids (Andrews and Simons, 1977; Fleagle, 1983, 1999) and was originally compared to hylobatids on the basis of overall limb proportions (Langdon, 1986)[13]. In many aspects of its forelimb morphology (most particularly humeral torsion of 108°, and articular features of the distal humerus and proximal ulna) it resembles *Ateles*, and similarly *Dendropithecus* may have been a suspensory climber (Harrison, 1982; Fleagle, 1983; Langdon, 1986). *Dendropithecus* appears to show, however, a mosaic of ceboid features with the forelimbs convergent on the suspensory atelines, and hindlimbs

[13] Although Harrison (1987) suggests that postcranial material from *Dendropithecus*, and probably *Micropithecus* and *Limnopithecus* as well, show none of the distinctive characteristics that are found in modern apes.

convergent on the Pithecinae (*Chiropotes* and *Cacajao*) (Rose, 1983). These latter genera frequently utilise hindlimb suspensory postural behaviours, but lack a prehensile tail. Although there is no direct evidence for pedal suspension in *Dendropithecus*, this convergence might indicate postural suspension involving both hind- and forelimbs (Rose, 1983). Retention of primitive anthropoid features throughout the skeleton indicates that quadrupedalism and climbing were also primary modes of locomotion for this species.

From the few postcrania that have been found for *Kalepithecus*, *Limnopithecus*, *Micropithecus* and *Simiolus*, it has been inferred that these genera have similar postcranial features to *Proconsul* (most particularly features of the humeroradial joint and the radial head consistent with quadrupedalism). They have also been found to share postcranial charcters with *Dendropithecus*, and thus similar locomotor patterns have been inferred for these species (Rose, 1996). These taxa have also been reported to be most similar to extant generalised platyrrhines utilising arboreal quadrupedalism, with perhaps elements of bridging and suspension within their positional repertoires (Rose et al., 1992; Rose, 1996).

The *Morotopithecus* vertebra UMP 67.28[14], on the other hand, is clearly more ape-like in its torso morphology (shorter cranio-caudally and broader medio-laterally), showing greater adaptation to orthogrady, quadrumanous climbing and bridging, transferring and below-branch locomotor behaviours (Sanders and Bodenbender, 1993). Unfortunately, it is impossible to make sweeping inferences of lumbar vertebrae number and vertebral column length from this isolated specimen, but it does provide the oldest example of a hominoid-like vertebral organisation, possibly indicating new patterns of substrate utilization (Sanders and Bodenbender, 1993).

What is most apparent from an examination of the early Miocene postcranial evidence is that the patterns of locomotion among the hominoids of this epoch were quite unlike those seen in hominoids today. The literature would suggest that

---

[14] Assigned initially to *P. major* [Walker and Rose, 1968], tentatively included in the Afropithicini by Sanders and Bodenbender [1993], and more recently renamed as *Morotopithecus* [MacLatchy et al., 2000].

most species were predominantly arboreal quadrupeds, with the exception perhaps of *Morotopithecus* (Ward, 1998). This would account for the extraordinary combinations of features seen in these genera, unmatched by any extant primate species. The one trend that appears to be true for all the genera examined, however, is that of powerful climbing and grasping capabilities. This observation would accord with the hypothesis suggested by Fleagle (1976; Fleagle et al., 1981) that the forelimb and torso morphology of the extant apes (and the convergent Atelinae) is more an expression of early adaptation to quadrumanous climbing, than specifically to brachiating, suspensory locomotion, although the concept of 'climbing' itself creates it own ambiguities.

LOCOMOTOR HYPOTHESES

Since the earliest analyses of Miocene hominoid postcrania, theorists have attempted to reconstruct the locomotor and postural behaviours of these genera, with a view to understanding the evolution of both hominid bipedalism and the very specialized forms of locomotion exhibited by other hominoids today. Due to the derived nature of extant hominoid postcrania, it was a reasonable expectation that the early species might share some of these features, thereby uniting the superfamily based upon postcranial synapomorphies (Ward, 1998). This may also have shed some light upon the circumstances of the initial cercopithecoid - hominoid split, perhaps with the invasion of different niches, and thus the reasons for the emergence of novel adaptations.

All extant hominoids possess a suite of postcranial synapomorphies (in the forelimb, hindlimb, thorax, pelvis and vertebral column) that contribute to several functional complexes: increased ability for raising the forelimbs above the head, increased potential for extension of the forelimb at the elbow, greater overall rotation of the forelimb, more flexibility at the wrist, a tendency towards erect posture during locomotion, greater mobility at both the hip and ankle joints, and differential usage of the forelimb over the hindlimb (Harrison, 1987). These specialisations have generally been associated with changes in locomotor behaviour from generalised arboreal quadrupedalism, to more flexible forelimb dominated quadrupedal climbing, bridging and suspension (Harrison, 1987;

MacLatchy and Bossert, 1996; Ward, 1998). Unfortunately, as the literature suggests, the early Miocene forms lacked many of the fundamental features characteristic of extant hominoids, although increased potential mobility at most joints of the appendicular skeleton was evident in many of the early species. Moreover, despite possessing similarities in their postcrania, the extant hominoids display fundamentally different postural and locomotor repertoires from one another, and thus constitute a poor comparative group for the inference of the locomotor capabilities of fossil forms.

One of the biggest dangers in comparative analysis is that of assuming overall morphological (and thus behavioural) similarity of fossil taxa to both extant genera and other fossil forms, from isolated elements of postcrania (Morbeck, 1983)[15]. The fossil record is by nature incomplete, and differential preservation means that complete specimens are rare (Ford, 1988). This is particularly relevant to the study of the Miocene forms, where countless studies have shown them to have no precise extant analogues (Rose, 1983; Walker & Pickford, 1983). Many fossils are distinct from extant forms in their combinations of primitive, derived and unique traits. This creates a "noise of traits" (Ford, 1988: 158) from which it is sometimes difficult to ascertain functional significance. Primitive traits may have become non-functional, or be adapted for different functional roles, and these features are not good indicators of behavioural capabilities. It is important, therefore, to identify derived traits, which are most crucial in elucidating behavioural capabilities in fossil forms (Ford, 1988; see also Ward et al., 1997).

The only method by which studies of this nature can be adequately carried out is the examination of fossil species for which good comparative material is available, or by analysis of features that can be securely linked to a single locomotor type (Day; 1979; Morbeck, 1983). The latter has been an underlying problem in the study of hominoid postcrania, where analysts have continued to disagree on the adaptive significance of derived hominoid traits. As a consequence, comparative analyses have differed in their interpretations of

[15] Oxnard (1963) also warns of the dangers of making inferences from isolated characters that can be 'specially selected' for their similarities to extant groups and locomotor categories.

features seen in the Miocene forms. The main hypotheses that have variously been postulated for derived hominoid postcranial features are: brachiation (Lewis, 1971a, 1972a-b, 1974), knuckle-walking (Conroy and Fleagle, 1972), vertical climbing (Fleagle et al., 1981; Fleagle, 1983; Rose, 1983; Langdon, 1986; Sarmiento; 1988; Begun et al., 1994; Gebo, 1996), and slow, deliberate quadrupedalism (Cartmill and Milton, 1977; Sarmiento, 1998; Kelley, 1997).

In an evaluation of the credibility of these hypotheses, a few fundamental criteria must be addressed. Firstly, if suites of characteristics are to be considered as synapomorphies of a group (for example, hominoids), then those features must be evident in all of the members of the group, but not in other groups. Secondly, for morphological characteristics to be functionally attributed to particular behaviours, the traits must show the same functional role, pertaining to that behaviour, in all of the taxa that exhibit them (Kay and Covert, 1984). Additionally, it should also follow that all of the taxa that include the behaviour within their locomotor repertoires should exhibit the adaptive characteristics[16]. Kay and Covert (1984) propose four criteria which need to be satisfied when attributing functional significance to traits in fossil taxa: there must be an extant analogue for that trait, the trait must have the same adaptive in role in all extant species that possess it, there must be no evidence to suggest that the trait evolved before the role for which is adaptive (see also Ford, 1988), and the trait must have a functional relationship to a particular adaptive role.

Brachiation hypothesis

Perhaps the most criticised of the different hypotheses is that which explains derived hominoid postcranial traits as adaptations to brachiation. Modifications of the hominoid wrist pertaining to ulna deviation were initially equated with the emergence of brachiation as a new locomotor pattern (Lewis, 1971a, 1972a-b,

[16] The problem with this latter criterion is found where distantly related groups adapt in fundamentally different ways to similar behaviours. This is most evident among the suspensory primates of the New and Old Worlds, where the atelines have adapted to below-branch activities with the assistance of their prehensile tail, which has essentially become a 'fifth limb'. It could be argued, however, that the locomotion utilised by the atelines is fundamentally different from that of the suspensory hominoids, and it then becomes a matter of classification: whether suspensory behaviour is evaluated as an all encompassing group, or divided into more descriptive sub-groups.

1974). This adaptation facilitates the hand's rotation of the radius around the ulna, increasing the extent of supination/pronation of the forelimb. Lewis considered these features to be essential in adaptation to brachiating locomotion, particularly that of slow bimanual suspensory locomotion. These wrist specialisations are unique to the Hominoidea, which demonstrates the monophyletic character of the superfamily, and is supported by the fact that there is no parallel in New World monkeys (Lewis, 1971b).

The fundamental flaw in this hypothesis is the sweeping assumption that all hominoids are 'brachiators'. As has been noted in a previous chapter, the hominoids are all quite different in their locomotor repertoires, ranging from 'true brachiation' in the hylobatids to quadrumanous climbing and clambering in *Pongo*, terrestrial knuckle-walking in the African apes and bipedalism in humans. The ape taxa exhibit unique adaptations for their specific modes of locomotion, and the hylobatid wrist differs from those of the great apes. Thus, the brachiation hypothesis is questionable purely on the basis that gibbons/siamangs and African apes use entirely different modes of locomotion from one another (Conroy and Fleagle, 1972; Fleagle et al., 1981).

All of the apes (with the exception of humans), however, do incorporate an element of suspensory behaviour into their locomotor repertoires, and perhaps it has been an issue of semantics as to what constitutes 'brachiating' behaviour. But, the fact that the semi-brachiators (as described by Napier and Napier, 1967) possess none of the specific 'brachiator' wrist adaptations, and the fact that the hylobatids have the least derived morphology, somewhat negates the possibility that the unique traits are fundamental to suspensory behaviour. If ulna deviation is indeed a brachiating adaptation, it seems odd that the least brachiating taxa are best adapted, and vice versa (Conroy and Fleagle, 1972; Sarmiento, 1988). Furthermore, analysis of the fossil material has shown that the early apes do not exhibit the suite of features than one would expect of a suspensory animal, and more specifically of a brachiator (Fleagle, 1983; Rose, 1983, 1997; Begun et al., 1994;). Thus, we can assume that, whilst the extant hominoids probably all possess features pertaining to suspensory locomotion (to different degrees), these

adaptations probably post-date the earliest hominoids and thus cannot be considered to be the initial hominoid postcranial adaptation.

Knuckle-walking hypothesis

Another hypothesis that has been promoted for the locomotor adaptations of early hominoids is that of knuckle-walking. *Pan* and *Gorilla*, as semi-erect quadrupeds, possess unique adaptations to their characteristic 'knuckle-walking' quadrupedalism. Among these, ulnar deviation facilitates adduction to the ulnar side of the wrist, necessary for this mode of locomotion (Conroy and Fleagle, 1972). Although Lewis (1971a) claimed that the hominoid wrist is less well adapted for supportive functions (due to ulnar deviation), this is clearly not the case, as African apes transmit most of their vast body weight through the wrist during knuckle-walking behaviour (Conroy and Fleagle, 1972). Reduction of the ulna styloid process, and the presence of a wrist meniscus, hence can be considered as morphological features allowing maximum flexibility at the joint, without reducing its ability to withstand compressive forces, which would thus be adaptive for knuckle-walking quadrupedalism (Conroy and Fleagle, 1972).

Moreover, similarities of the *D. (Proconsul) africanus* wrist to extant hominoids are found in combination with quadrupedal and terrestrial features and therefore this early Miocene species might have been adapted for knuckle-walking (Conroy and Fleagle, 1972)[17]. The gibbon, in contrast to both the great apes and the fossil species, is more monkey-like and thus more primitive, and a knuckle-walking hypothesis would explain this limited adaptation in hylobatids (Conroy and Fleagle, 1972).

The knuckle-walking hypothesis has been strongly criticised (Morbeck, 1975; Jenkins and Fleagle, 1975; Fleagle et al., 1981; Fleagle, 1983; McHenry and Corruccini, 1983). Primarily, the proponents of this theory make the same fundamental error as those promoting the brachiation hypothesis. Gibbons do not

[17] Zwell and Conroy (1973) suggested that this species may have been an 'incipient' knuckle-walker, utilising hand postures where weight was supported on the heel of the hand and the dorsal surfaces of the phalanx.

knuckle-walk, yet show evidence of change from the monkey type of wrist morphology towards an African ape wrist. If knuckle-walking was the function for which the unique wrist morphology was derived, then one would predict that gibbons should be incipient knuckle-walkers. This is clearly not the case. Furthermore, the early hominoids show none of the morphological specialisations that would be expected for knuckle-walking locomotion (Morbeck, 1975; Beard et al., 1986)

In short, neither of the above hypotheses addresses the question of the initial adaptation, which should be common to all species that exhibit ulnar deviation and the associated features of the carpus. Evidently, the unique adaptations of the wrist are adaptive for both brachiation and knuckle-walking, and it may be reasonable to assume that both behaviours could have evolved from a similar adaptive base, perhaps a more primitive form of locomotion different from that of extant quadrupedal monkeys, from which both of these specialised forms of ape locomotion could easily have derived.

Additionally, both brachiation and knuckle-walking are associated with changes in forelimb anatomy and thus may provide sufficient explanation for the evolution of forelimb traits, but they do not adequately address the adaptations towards enhanced mobility in the joints of the hindlimb. It would be reasonable to expect, therefore, that the locomotor behaviour of the basal hominoids would incorporate the use of all four limbs in a wide variety of postures, on irregularly placed substrates, to warrant the increased mobility seen in all of the joints of the appendicular skeleton. The phalanges of proconsulids suggest less difference between the grasping capabilities of the hands and feet in *Proconsul* than typically seen in the extant hominoids that utilise more forelimb dominated locomotion; early apes probably incorporated a significant amount of quadrupedal grasping into their locomotor repertoires, with the hindlimbs undertaking a powerful grasping, rather than propulsive, role (Begun et al., 1994).

Furthermore, knuckle-walking and brachiation are both highly specialised forms of locomotion, utilised by specific taxa: African apes and *Hylobates*, respectively (Langdon, 1986). It is argued that these behaviours are too specialised to

constitute reasonable models for the ancestor of bipedal hominids, and thus neither would represent a reasonable analogue for the primitive hominoid locomotor type, either (Langdon, 1986). A common hominoid ancestor would have to possess features that are shared by all the living genera, and which might pertain to a tendency to orthograde postures, and general arboreal vertical climbing (Langdon, 1986)[18], or to slow deliberate quadrupedalism (Kelley, 1997). Also the morphological traits exhibited by hominoids are convergent in other genera (for example lorises, and to a certain extent atelines) that do not utilise such behaviours, and thus it would be logical to assume that the underlying locomotor function of such characteristics would be one undertaken by all of the genera possessing such features.

The most likely locomotor types that have been advocated as providing a base for the evolution of all hominoid specialisations are vertical climbing or slow, deliberate quadrupedalism. The major problem in the analysis of such hypotheses is that many studies consider climbing behaviour in its entirety, rather than making the distinction between different forms of climbing and consequently, it is confusing when these two behaviours are treated as synonymous (Gebo, 1996). Both vertical climbing and slow, deliberate quadrupedalism could be incorporated within a 'climbing' classification and, ostensibly, both would demand similar levels of mobility in both the fore- and hindlimbs. Pronograde and orthograde behaviours, however, would require different modifications of the torso which should be apparent in genera that engage in these behaviours with relative frequency.

For the purposes of this study, however, vertical climbing will be restricted to a definition that suggests orthograde postures, accompanied by forelimb 'hoisting' and hindlimb propulsion, whilst slow, cautious quadrupedalism will be defined as deliberate progression, primarily along horizontal or oblique supports, generally with three extremities contacting the support at any one time during movement.

---

[18] Langdon's reasoning would not necessarily exclude a slow-climbing hypothesis, which would also provide a more generalised form of locomotion from which specialisations could have derived, although this would entail less use of orthograde postures.

Vertical climbing hypothesis

The vertical climbing hypothesis claims that features of the ape forelimb anatomy that have often been designated as brachiating adaptations can just as well be explained as adaptations to vertical climbing (Fleagle et al., 1981). The forelimb musculature of atelines and apes is more active during climbing and hoisting behaviours than during brachiation, and bone strain tests on ulnae suggest brachiation and climbing show similar magnitudes of force (Fleagle et al., 1981). Additionally, Sarmiento (1988) argued that the midcarpal joint in early hominoids (as in *Hylobates*) lacks the ability to withstand forces from different directions within the palmar plane, and is therefore probably not often used when support points are below the centre of gravity (quadrupedal on horizontal supports), thus supporting the interpretation of more orthograde body postures in these genera.

Furthermore, a human ancestor primarily adapted for climbing would show other elements of forelimb morphology comparable to that previously associated with brachiation, and a hindlimb morphology that would be both morphologically and functionally pre-adaptive for bipedalism (Fleagle et al., 1981). Thus, brachiation does not necessarily constitute a fundamental part of ape and human ancestry. This 'climbing hypothesis' would also account for the fact that 'brachiating adaptations' have been noted in non-brachiating primates, and explains the presence of these features in the great apes, which seldom utilise brachiating behaviour.

In a recent study, Gebo (1996) considered the relative merits of the various hypotheses (vertical climbing, slow climbing, brachiation, and knuckle-walking models) postulated as explanations for the ape body plan, in an attempt to elucidate the origins of human bipedalism. In particular, he evaluated the frequency of climbing, and vertical climbing, locomotor behaviours across a wide spectrum of extant primates.

Gebo (1996) negated the possibility that brachiation might be responsible for the unique ape characteristics. Whilst the atelines and apes, both of whom utilise frequent overhead arm positions, share similar morphological features of the

upper limb and thorax, ulnar deviation is limited in atelines, which would suggest that parallel evolution of the shared features probably occurred between these two groups[19]. The fact that lorises share some of the derived ape characteristics of the wrist also somewhat refutes the possibility that these features are functionally related to brachiation. On the other hand, lorises and African apes do not utilise bridging and transferring behaviours, which are a major component in the orangutan repertoire, and thus this too seems an unviable explanation for the unique characteristics (Gebo, 1996)[20].

Only a few primates use vertical climbing with any great frequency; gorillas and chimpanzees utilise this form of locomotion infrequently (except *Pan paniscus*), orangutans and gibbons use it more so, although usually during feeding. The only other primates that regularly climb vertical supports are *Alouatta seniculus*, *Ateles* and *Cercopithecus ascanius*, again during feeding activity. Although some Old World monkeys use vertical climbing, they are not particularly 'well-adapted' due to their limited joint mobility throughout their appendicular skeleton (Gebo, 1996).

Although African apes are not noted to be frequent climbers, and therefore are seemingly bad models, the perceptions of this particular behaviour are fundamentally obscured by the large terrestrial component to African ape travel (probably associated with their large body size) (Gebo, 1996). When statistics are taken purely from their arboreal behaviour, African apes are found to be frequent climbers, particularly on vertical supports. Indeed, if only the arboreal component of locomotion is considered, gorillas, chimps, *Macaca fascicularis* and *Papio anubis* all engage in significant amounts of vertical climbing. In fact, *Gorilla* and *Pan* use this behaviour more than *Pongo* when in an arboreal environment (Gebo, 1996).

---

[19] Atelines also possess their own derived characteristic, their prehensile tail, and consequently they have their own quite unique form of five-limbed suspensory locomotion.
[20] Gebo (1996) somewhat contradicts himself towards the end of his paper by suggesting that these behaviours might be a good arboreal model for an ancestral protohominid morphotype for locomotion during travel bouts.

The majority of studies, however, make no distinction between different forms of climbing (Gebo, 1996). Vertical climbing, in its essence, is only practised up and down vertical supports, and therefore cannot be a regular component of locomotion during travel. Most primates travel either quadrupedally or by leaping. Orangutans use quadrumanous scrambling, brachiation and tree-swaying, and a *Pongo*-like locomotor type might represent a good model for a basal hominoid utilising climbing within its locomotor repertoire (Gebo, 1996).

In conclusion, Gebo (1996) recommends that climbing and the morphological adaptations to it were the most likely primitive hominoid adaptations, and that *Proconsul* and the other early Miocene genera were arboreal quadrupeds, but also adept vertical climbers/clamberers. He proposes, however, that vertical climbing itself probably post-dated the divergence of gibbons, due to its apparent infrequency in hylobatids, which somewhat contradicts the notion that it could be ancestral for hominoids.

If it is reasonable to include the African apes within a 'vertical climbing' group, due to their high levels of this behaviour during their limited arboreal activity, then surely one would expect to see similar morphological adaptations in the other genera that utilise vertical climbing to similar degrees (i.e., *Cercopithecus ascanius*, *Macaca fascicularis* and *Papio anubis*). This is not evident from the morphological literature reviewed. Additionally, Gebo's (1996) assumption about the adaptations post-dating *Hylobates*, due to the apparent infrequency of the behaviour in this genus, seems to be dubious, as the hylobatids utilise this behaviour to a greater extent overall than the African apes, but less so when the purely arboreal locomotor/postural component was examined. There is no reason to negate the possibility that all of the hominoids have derived from a common base. Even minor spells of a particular activity could be indicative of potential, and perhaps of a more frequent ancestral component.

It seems that vertical climbing would be a good model for an ancestral hominoid, as all hominoids utilise a degree of this behaviour within their locomotor and postural repertoires. It would also form a reasonable basis for the derived locomotor types of hominoids today. The main criticism of this theory, however,

is that there is no anatomical evidence to support orthograde postures in the early Miocene genera (Ward et al., 1993; Kelley, 1997). This is most evident in the torso, which most resembles that of pronograde arboreal quadrupeds (Ward, 1993).

Cautious quadrupedal hypothesis

Perhaps the most popular hypothesis among theorists today is that of an adaptation to cautious quadrupedalism among the earliest hominoids. This has been supported by countless postcranial studies of the Miocene apes (see above) that have shown that these early apes exhibit a quite primitive locomotor anatomy compared to the more specialised extant apes, combining large bodies with a monkey-like torso, increased overall mobility in the appendicular skeleton, and loss of tail.

Most authorities recognise the lack of brachiating (or indeed suspensory) characteristics in the early Miocene forms, and there is no evidence to support knuckle-walking in these genera. Although the early Miocene forms have been described as generalised pronograde quadrupeds, they (most particularly *Proconsul*) are known to share a number of postcranial features with extant hominoids, most of which pertained to increased joint mobility (or stability) over a greater range of motion, increased grasping ability in both hands and feet, and loss of tail (Kelley, 1997). Many postcranial studies have supported a view that the early Miocene genera were powerful, slow-climbing quadrupeds, possibly with an element of below-branch forelimb assisted climbing (Aiello, 1981; Conroy and Rose, 1983; Rose, 1983, 1996; Walker & Pickford, 1983; Langdon, 1986; Leakey et al., 1988b; Begun et al., 1994).

Analysis of the wrist morphology of lorises (*Perodicitcus*, *Nycticebus*, *Loris* and *Arctocebus*), has found that these taxa share a number of features with extant apes that have previously been described as hominoid synapomorphies related to brachiation (Cartmill & Milton, 1977). The convergence between these two very different primate groups implies a shared functional specialisation. Undoubtedly, this can be neither brachiation nor knuckle-walking since lorises do not include

either of these specialised behaviours within their repertoires. As discussed earlier, lorises are characterised by slow, deliberate quadrupedal locomotion, necessitating enhanced pedal and manual grasping capabilities and a large range of mobility in the limb joints, particularly mediolateral rotation of the feet and hands around the long axis of the limbs, in an accommodation to inclined supports (Grand, 1967; Walker, 1969; Cartmill and Milton, 1977). These features in hominoids can be credibly associated with slow, deliberate, quadrupedal locomotion (climbing and bridging) in ancestral apes, which would provide a morphological base for the evolution of the more specialised forms of locomotion seen in extant apes (Cartmill and Milton, 1977)[21]. Brachiation or knuckle-walking adaptations, therefore, might have evolved from a cautiously moving quadrupedal ancestor, rather than one utilising a hylobatid type of suspension.

This suggestion would accommodate all of the observed features in the early Miocene forms. Large body size and loss of tail would be disadvantageous for an arboreal animal in terms of retention of balance, and powerful grasping capabilities would compensate for this weakness. A well-developed grasping capability would necessitate a larger range of mobility in the limb joints, particularly at the ankle and wrist, but this would be at the expense of stability at these points. With reduced stability, joint surfaces would have to be robust to accommodate unpredictable stress orientation, and locomotion would be necessarily cautious.

Kelley (1997) suggests that the main keys to *Proconsul* locomotion are the emergence of the evolutionary novelties: absence of tail and powerful opposable thumb. For a tailless and large bodied quadruped, in an arboreal environment, one of the biggest problems would have been one of balance. Powerful grasping, facilitated by increased joint and overall limb mobility, might therefore have

---

[21] Sarmiento (1988) also suggested the early hominoids to be similar to the lorisids, proposing the traits seen in these early genera to be associated with mid-carpal ulna deviation, loading of the mid-carpal joint in varying degrees of adducted and abducted postures, reduced emphasis on ulnocarpal loading and strong flexion of the flexed wrist. "As they pertain to locomotor behaviours, these functions in mammals are associated with cautious climbing" (Sarmiento, 1988: 335). He concludes, however, that early hominoids were most likely vertical climbers, which is in a sense contradictory, as the lorisines are not definitively vertical climbers, but are characterised by slow quadrupedal progression.

evolved primarily to compensate for the loss of tail. Thus, the distinctive postcranial features of the early Miocene hominoids may represent nothing more than compensation for the loss of the tail[22]. In such a scenario, the first hominoids may have been no more than large "arboreally compromised" catarrhines (Kelly, 1997).

It is primarily this latter theory that is under scrutiny in this study, by means of a comparative analysis of the wrist and ankle joints of 'slow-climbing' lorisids and extant hominoids. These specific anatomical regions are fundamental to this particular locomotor type, in that they are necessary prerequisites for the ability to grasp in a wide range of orientations. This enhanced mobility is highly dependent upon the structure and congruency of these joints. The aim is to ascertain if these groups exhibit comparable structures of these joints, which then could be interpreted as underlying adaptations to slow-climbing locomotion. Although many detailed examinations of the wrists and ankles of these taxa have been conducted in the past, and a thorough comparative study was undertaken on the wrist by Cartmill and Milton (1977), previous analyses have taken each joint in isolation, rather than as a functional whole contributing to overall mobility for grasping in all four limbs.

[22] Although this suggestion is perhaps the most plausible reconstruction of early hominoid evolution, it says nothing about the order of acquisition of the different characteristics. It seems to imply that the first adaptation was that of tail loss, with the further derived features evolving to compensate. There is no explanation for why the tail was lost in the first place, which could be maladaptive for large bodied primates in a precarious arboreal habitat.

CHAPTER3

Wrist and ankle morphology

EXTANT HOMINOID WRIST MORPHOLOGY IN A COMPARATIVE CONTEXT

Wrist morphology has emerged as an important component in the study of primate adaptations and evolution, most particularly in the study of the early emergence of hominoids (e.g. Lewis, 1971a, 1972a-b, 1974). It must be noted, however, that the complex structure of the wrist and the vast array of hand functions makes it difficult to interpret primate carpal structure in phylogenetic or adaptive contexts. Consequently, there is little agreement on how primate wrist anatomy impinges upon issues of systematics, evolution or function (Jenkins, 1981).

Primates in general have a primitive mammalian wrist configuration, with the retention of the contact between the ulna and the carpus, as the lower extremity of the ulna articulates directly with the pisiform and triquetral (Lewis et al., 1970; Lewis, 1971a, 1972a-b, 1974). Among hominoids, however, the wrist joint is somewhat modified (Lewis, 1971a, 1972a-b, 1974; O'Connor, 1975). The ulna has become withdrawn from direct articulation with the carpus, and an intra-articular meniscus has developed in the interval between the distal ulna and the triquetrum and pisiform. In this manner, the ulna styloid process is, in varying degrees among the extant hominoids, almost completely excluded from direct participation in the wrist joint (Lewis, 1971a, 1972a-b, 1974).

The cercopithecoids are uniform in showing habitual dorsiflexion of the wrist during locomotion, using either palmigrade or digitigrade substrate contact (O'Connor, 1975). In these taxa, like other primitive quadrupedal mammals, the ulna articulates directly with both the pisiform and the triquetral. The triquetral in ceboids and cercopithecoids is large and block-like, articular on its anterior margin with the elongated pisiform, which in turn projects back to form the 'heel' of the hand in these quadrupedal taxa (Lewis, 1971a, 1972a-b, 1974). Both the triquetral and the pisiform have clear, slightly concave facets on their proximal aspects for direct articulation with the ulna. Similarly, the ulna styloid process has

a large convex articular surface on its distal extremity, and facing the interior of the joint, with the opposite peripheral aspect, facing laterally in quadrupedal postures, non-articular (Lewis, 1971a, 1972a-b, 1974). Together, the contact between the pisiform and triquetral forms a receptive, weight-bearing cup for the tip of the ulna styloid process, which abuts tightly against the side of the ulna styloid process, restricting mediolateral mobility in this position, and limiting ulnar deviation ((Lewis, 1971a, 1972a-b, 1974; O'Connor, 1975). This is accompanied by a tightening of the other carpals in relation to one another, as the scaphoid presses against the inside of the radial styloid process and the lunate becomes rigid between the scaphoid and the triquetrum. Thus, when the wrist tends towards maximum dorsiflexion, movement is limited to flexion, with mediolateral deviation and axial rotation becoming increasing more difficult (O'Connor, 1975).

The articular facet on the ulna styloid process in *Pan*, however, is more peripheral in its orientation (i.e., dorsally placed rather than towards the interior of the joint), for contact with the meniscus, with a more or less distinguishable facet at the tip for the triquetral. Direct articulation of the styloid with the carpus is thus restricted by the presence of the intra-articular meniscus. The distal extremity of the ulna styloid process is also somewhat flattened, but sometimes hook-like in shape. The triquetral is reduced in size, taking the form of a triangular pyramid, and its concave palmar surface articulates with an enlarged convex facet on the dorsal aspect of the pisiform, which projects more distally into the palm (rather than back to form a 'heel'). The reorganisation of the carpus on the ulnar margin results in an opening out of the primitive articular cup formed by the adjoining triquetral and pisiform, into a wider and more convex surface, articular primarily with the meniscus although the triquetral retains a limited contact with the tip of the ulna styloid process (Lewis, 1971a, 1972a-b, 1974).

The construction of the wrist in *Gorilla* is much the same as that found in *Pan*, but with a more significantly reduced ulna styloid process, lacking a hook-like form, and articular on the reduced distal extremity. Similarly in *Pongo*, the ulna styloid process is much reduced, forming a short conical distally orientated projection,

with a reduced convex facet on the distal extremity for articulation with the triquetral (Lewis, 1972a-b, 1974).

In *Hylobates* the ulna side of the wrist joint is somewhat intermediate between monkeys and the other hominoids: monkey-like in the carpus and great ape-like in the ulna styloid process (Lewis, 1971a, 1972a-b, 1974). The hylobatid ulnocarpal joint contains a meniscus, but the shape and orientation of the triquetral and pisiform are more reminiscent of monkeys (although the pisiform is more distally directed as in the other hominoids, orientated down towards the palm). The ulna styloid process retains the primitive contact with the carpus, through the meniscus, and a small bony ossicle called the os Daubentonii is present within the meniscus, almost as an unattached extension to the pisiform. The ulna styloid process is generally hook-like, and the articular facet for the carpus is orientated distally, but more towards the exterior of the joint (Lewis, 1971a, 1972a-b, 1974).

Thus, all living apes have variations on this novel type of wrist joint, in contrast to the other primates: withdrawal of the ulna from its primitive articulation with the carpus (triquetral and pisiform) with the ulna styloid process developing a neomorphic ulnar head (Lewis, 1971a, 1972a-b, 1974). *Hylobates* is somewhat intermediate between the great apes and cercopithecoids in this structure (Lewis, 1971a, 1972a-b, 1974; Conroy and Fleagle, 1972). The hominoid ulna head is expanded into large evenly convex structure, semi-lunar in shape from the distal aspect. The pisiform has two articular surfaces: one for the triquetral, and a second for the meniscus. The triquetral has two facets for the pisiform and the meniscus. The meniscal facets on both the pisiform and triquetral are generally convex and poorly defined, and often absent (O'Connor, 1975). The reorganisation of the wrist results in a realignment of the hand into the long axis of the forelimb, from the primitive position of habitual dorsiflexion. The apes exhibit a "progressive sequence" of wrist joint specialisation, which Lewis (1972a) suggests may possibly represent surviving stages of a true phylogenetic sequence, rather than varying grades of parallel evolution, perhaps documenting the stages of change from palmigrade to forelimb suspension.

Cercopithecoids are fundamentally adapted for palmigrade or digitigrade quadrupedalism; they are relatively uniform in their wrist anatomy, with little capability for mediolateral excursion at the wrist joint during locomotion. O'Connor (1975) suggests, however, that the structure of the cercopithecoid wrist allows for a wide range of behavioural variations. Having lost the primitive ulnocarpal articulation, hominoids are not specifically adapted for palmigrade locomotion, although some do employ this posture in certain conditions. Cercopithecoids, on the other hand, are not adapted for brachiation due to their limited mobility in the wrist joint (O'Connor, 1975).

Studies of New World semi-brachiating monkeys (*Ateles* and *Lagothrix*) have shown that these genera retain the primitive articulation of the wrist associated with quadrupedal locomotion, with both the pisiform and triquetral articulating directly with the ulna styloid process (Lewis, 1971b, Conroy and Fleagle, 1972)[23]. Lewis (1971b) proposed that the derived hominoid wrist configuration is correlated with an increased range of supination, suggesting that it may be indicative of evolutionary history of suspensory locomotor and feeding behaviour. Among non-hominoid primates, semi-brachiating monkeys are the most likely to exhibit parallel acquisition of these features, due similarities in their locomotor repertoire to suspensory extant apes, but this is not the case. Lack of flexibility of the wrist throughout suspensory locomotion among the atelines may well be compensated by the evolution of their prehensile tail (Lewis, 1971b). As Lewis' studies found no other group exhibiting similar features, he suggested the unique hominoid wrist complex to be monophyletic[24].

Studies of other joints within the wrist, however, have revealed striking similarities between the New and Old World suspensory genera (Jenkins, 1981). In an analysis of the structure of the midcarpal joint in New and Old World anthropoids (*Ateles*, *Lagothrix*, *Symphalangus*, *Hylobates* and *Macaca*), Jenkins

---

[23] This is contested by Youlatos (1996) who reports *Ateles* and *Alouatta* to have certain wrist features in common with hominoids. *Ateles* in particular is said to possess a modified ulnocarpal joint where the ulna does not articulate with the pisiform.

[24] Lewis (1971b) notes that previous authors had proposed brachiation to have evolved in parallel several times, on the basis of forelimb elongation, but in view of the lack of these particular wrist adaptations in the semi-brachiating monkeys of the New World, there is no evidence to support parallel evolution in this particular wrist adaptation.

(1981) found that the 'brachiators' differed from the quadrupedal genera in their configuration of the proximal articular facets of the capitate and hamate; the facets between the capitate and trapezoid; and the hamate facet for the triquetral. This suggests that parallel evolution of the structure of the midcarpal joint, towards increased rotatory capabilities at this joint, may have occurred between Old and New World brachiators. This, in turn, would support a functional role of midcarpal supination for suspensory behaviours. *Pongo*, which utilises significant amounts of below branch suspensory activities, exhibits similarities in the midcarpal joint to the brachiators, whilst *Pan*, predominantly a quadrupedal knuckle-walker, does not (Jenkins, 1981).

The many detailed analyses of primate wrist morphology (e.g., Lewis et al., 1970; Lewis, 1971a, 1972a-b, 1974; Cartmill and Milton, 1977) have emphasised the distinct differences in the shape, organisation and articulations of the ulna and the proximal carpus in hominoids and monkeys. Lewis (1971a, 1972a-b, 1974) proposed that the hominoid withdrawal of the ulna from the carpus, which results in limited (or absent) ulnocarpal articulation, a reduction in the ulna styloid process, and the presence of an intra-articular meniscus, constitutes a complete remodelling of the ulna side of the wrist. These changes are associated with increased capabilities for ulna deviation from the carpus, facilitating an increased range of pronation-supination of the forearm at this joint, where the radius and carpus rotate around the ulna to a greater degree (Lewis, 1971a, 1972a-b, 1974). All Hominoidea have an increased range of this movement (180°), compared to a more limited range in monkeys (90°) (Lewis, 1972b)[25]. Lewis (1971a, 1972a-b, 1974) suggested that the retreat of the ulna was an essential prerequisite for an increased range of supination-pronation, where the radius and carpus rotate around the ulna head, as the ulna styloid process is freed from its restricting articulation with the triquetral and pisiform. This new organisation of the

[25] O'Connor and Rarey (1979) also looked at the degree of pronation-supination possible in cercopithecoids, ceboids and hominoids through experimental studies. Their analysis found that ranges of radioulnar pronation and supination differed widely between hominoids and non-hominoid anthropoids, reflecting both the different locomotor repertoires, and the structures of the radioulnar joints. Their study found, however, that the presumably least derived hominoid, *Hylobates*, had the greatest range of rotation of the forearm (163°). This study, however, did not include *Pan* or *Gorilla*.

ulnocarpal joint is accompanied by further changes within the midcarpal joint for stability throughout a range of positions (Lewis, 1971a, 1972a-b, 1974; O'Connor, 1975).

Sarmiento (1988) supports Lewis's argument that characters of the hominoid wrist are modified primarily to facilitate forearm rotation, but suggests that the behavioural repertoires that were first associated with forearm rotation and the changes that led to specialisations of extant hominoids are unclear. Sarmiento (1988) noted generic differences between the uses and postures of the wrist joint in hominoids, and proposed that the behavioural differences seen among extant hominoids probably resulted in different wrist specialisations.

O'Connor (1975) proposed, however, that although the configuration of the wrist determined the degree of ulnar deviation at the ulnocarpal joint, it did not limit the range of pronation-supination, which was checked at the elbow joint. Although the suspensory locomotor repertoires of hominoids are often associated with an increased range of supination, and the changes in the wrist structure of hominoids may be advantageous for this, O'Connor found no cause and effect relationship between presence or absence of ulnocarpal articulation and amount of possible supination at radioulnar joint (one *Pan* specimen had 160° supination, 40° more than any cercopithecoids, despite the retention of significant ulnotriquetral articulation).

The suite of changes in the wrist of hominoids was initially correlated with the capacity for brachiation in hominoids (Lewis, 1972a-b; O'Connor, 1975). Lewis (1972a) proposed that this 'evolutionary novelty' might have formed the foundations for the emergence of the diverse suspensory positional repertoires found in modern apes today. Brachiation, as an early feature of hominoid evolution, may indeed have been fundamental to the initial divergence between hominoids and the other catarrhines, as new ecological niches could potentially be exploited (thin flexible branches through weight distribution). "There is a case for believing that improvement of a key morphological component, the wrist joint, opened up a whole new phase of primate evolution" (Lewis, 1972: 211).

Conroy and Fleagle (1972), however, disputed the proposition that the unique hominoid wrist joint was a brachiating adaptation, primarily because of the fundamental differences between the gibbon wrist and those of the African apes. The wrist of *Hylobates* is more monkey-like, which suggests that the wrists of *Pan* and *Gorilla* are not primarily adapted for brachiation. Ulna deviation cannot be primarily a brachiating adaptation, in view of the fact that the most frequent brachiator (*Hylobates*) is the least derived in its wrist complex (Conroy and Fleagle, 1972).

Conroy and Fleagle (1972) also argued against Lewis' view that the derived hominoid wrist was less adapted for supportive functions, suggesting that during knuckle-walking the gorilla transmits most of its weight through the wrist. Indeed, differences between the triquetral facet orientation on the hamate between monkeys and apes can be related to weight transmission at this joint (Spoor et al., 1991). In *Gorilla* and the monkey genera, this facet is orientated to present a relatively large effective surface for weight transmission, whilst in the other apes it is orientated more proximodistally; less effective for weight transmission but allowing a wide range of deviation in the midcarpal joint. As a result, the potential for ulnar deviation at the midcarpal joint, as far as the hamate is concerned, depends on the length and orientation of triquetral facet. A short facet with radioulnar orientation equates with limited deviation, and a distal concave end of the triquetral facet prevents excessive ulnar deviation at the midcarpal joint (Spoor et al., 1991).

From an evaluation of the literature it becomes clear that there are fundamental differences between the structures of the wrist of hominoids and cercopithecoids, with atelines showing a mosaic of Old World monkey and ape characteristics; a primitive morphology in the ulnocarpal joint but converging on the hominoids in the midcarpus. The difficulty arises in elucidating the functional significance of the variation. It is evident that the morphological differences are consistent with the locomotor and postural variation between these groups, but it seems that the discussion has been somewhat obscured by the fundamental differences of opinion as to the underlying locomotor adaptations of hominoid genera. This is

hindered by the rather extreme specialisations of hominoids, which make it difficult to determine the functional relevance of characters for the superfamily as a whole.

EXTANT HOMINOID ANKLE MORPHOLOGY IN A COMPARATIVE CONTEXT

The anatomy of the primate foot has been well studied, and, like the wrist, it has important implications for the understanding of both primate adaptation and the evolution of locomotion. The primate foot is adapted for multiple functions (weight-bearing, propulsion, suspension and prehension), and in primates the structure of the foot reflects the differential importance of these uses, as a result of the variation in positional and locomotor behaviours across the order (Langdon, 1986). The foot has generally played a smaller role than the wrist in the debate about early hominoid locomotor adaptations, because much of the focus has been directed towards the role of forelimb dominated locomotor patterns such as knuckle-walking and brachiation. There has been considerable discussion, however, regarding the differences between the foot morphologies of palmigrade and more orthograde quadrupeds, in the inference of the locomotor precursor to bipedalism. Inevitably, hominoid movement capabilities of the foot have been central to these discussions.

In his comparative analysis of the Miocene hominoid foot, Langdon (1986) looked at the anatomical structures in extant forms, with a view to creating a broad classification of foot morphology for the different positional categories. Langdon's study found several differences between the ankle joints of hominoids and monkeys, which fundamentally pertained to increased overall mobility in the ape foot, and limited mobility in monkeys (see also Strasser, 1988). The study also found similarities between the apes and atelines, however, which may reflect homoplasies between the more suspensory genera of the Old and New Worlds.

The three main components of the primate ankle joint that pertain to differential mobility are the talocrural joint, the subtalar joint and elements of the midtarsal joint. The talocrural joint provides the articulation between the foot and the rest of the skeleton, and is formed by the talus secured within the mortise frame of the

malleoli of the distal tibia and fibula. The main direction of movement permitted at this joint is plantar/dorsiflexion, as the distal tibia and fibula travel over the joint from a posterior to an anterior position. The talar trochlea tilts medially towards the rear, resulting in lateral rotation and inversion of the foot in dorsiflexion. Further accessory motions (mediolateral rotation and inversion/eversion) are possible to varying degrees in different primates, dependent largely upon the shape of the talar trochlear, and its congruence with the tibial and fibular malleoli (Lewis, 1980a; Langdon, 1986).

The subtalar joint comprises the two articulations between the talus and the calcaneus: the anterior and posterior talocalcaneal contacts. The primary movement at this joint is that of inversion/eversion, with accessory abduction/adduction and plantar/dorsiflexion contingent principally upon the obliquity of the subtalar axis relative to the long axis of the foot. The action at this joint is of utmost importance in adaptation of the foot to irregularly orientated substrates in an arboreal environment, and it would be expected that climbing and suspension would necessitate a greater degree of flexibility within this joint, indicated by a more oblique subtalar axis. Conversely, cursorial or saltatory genera would require more stability, which would be reflected by less obliquity of the axis at this point (Barnett, 1970; Langdon, 1986).

The midtarsal joint involves the talonavicular and calcaneocuboid articulations, and movement occurs about two axes: the longitudinal axis is related to inversion/eversion of the anterior part of the foot, whilst the oblique axis allows mediolateral rotation and flexion/extension within the foot (Langdon, 1986). For the purpose of the present study, the most important element in this articular complex is that of the talonavicular contact, and how the shape of the talar head may relate to overall mobility at this point.

The talocrural joint is of remarkably uniform design in anthropoids, in terms of the general structure of the bones, the mediolateral orientation of the joint axis, the range of excursion and the packing of the bones (Lewis, 1980a; Langdon,

1986)[26]. Despite this, minor differences in the shape of the trochlea (in particular the depth of the trochlea, the sharpness of the medial and lateral crests, and the obliquity of the tibial malleolar facet) allow for varying degrees of mediolateral rotation and inversion/eversion at this joint (Langdon, 1986).

In cercopithecoids, the trochlea is high in relation to the rest of the talus, with highly curved arcs and a deep trochlear trough. These taxa also have a high degree of trochlea asymmetry, with the lateral crest substantially higher than the medial, most particularly in terrestrial forms, and a relatively high degree of anteroposterior trochlear wedging (Strasser, 1988). Overall, these features imply that the contact between the talus and the distal tibia and fibula is relatively close-fitting, and thus secondary movements in a mediolateral plane are limited. The relatively high degree of trochlea wedging, however, suggests that the cercopithecoids have differential accessory mobility in dorsiflexed and plantarflexed postures. Stability is maintained during quadrupedal locomotion, however, as cercopithecoids use habitually dorsiflexed foot postures when engaging in this behaviour. This suite of talocrural features is consistent with what might be expected for quadrupedal runners and leapers, where mobility would be traded off for stability at speed. As a consequence, the joint components would be less robust with a greater predictability of force direction (Langdon, 1986; Strasser, 1988).

In the African apes, the trochlea is narrow and anteroposteriorly wedged, the most extreme wedging found in *Gorilla*. This wedging changes the relationship between the trochlea and mortise formed by the tibial and fibular malleolar facets during the excursion of joint. As a result, the joint retains a close-packed stability during dorsiflexion, but becomes looser and thus more mobile in plantarflexion. The degree of mobility in this latter position is proportional to the extent of wedging, or the difference in breadth of the anterior and posterior extremities of the trochlea. A high degree of wedging was also apparent in the atelines, but not in the other New World monkeys (Langdon, 1986; Strasser, 1988).

---

[26] Lewis (1980a) found distinctly derived talocrural morphology in *Homo sapiens*, compared to the universal, primitive pattern exhibited by the other primates.

The African ape trochlea is relatively shallow with rounded, less well-defined crests, and a low medial arc. The medial malleolar facet in these hominoid genera is also set quite obliquely in relation to the superior surface of the trochlea (rather than the more vertical facets found in monkey genera). All of these features contribute to a less restrictive articulation at the talocrural joint, and thus a greater range of accessory motion. These features would correspond to the increased demands for mobility of the foot in scansorial or suspensory genera, at the expense of both stability and speed. The forces incurred by different orientations of the foot in an unpredictable arboreal environment would be multi-directional, and thus this would necessitate a talus that was robust overall (Langdon, 1986).

In *Pongo*, the trochlea is relatively wide, with an oblique malleolar facet, but is moderately less wedged, with a deeper trough, than in the other great apes. This greater depth of the trochlea is paralleled in the suspensory atelines, which perhaps does not concur with the expectations for taxa that require a significant amount of accessory abduction/ adduction in the ankle joint during four-limbed suspensory behaviours. Langdon (1986) suggests, however, that trochlear depth would be largely irrelevant during traction, having minimal effect on the overall flexibility of the joint in these postures, but it would offer increased stability in more weight-bearing positions.

The trochlea of *Hylobates* is intermediate in its characteristics between the cercopithecoid and African ape types. The trochlea is relatively very narrow, showing high arcs and low wedging, in combination with shallow depth of the trochlear trough and obliquely set malleolar facet (Langdon, 1986).

Overall, the cercopithecoids exhibit both a higher degree of wedging and greater asymmetry than both *Hylobates* and non-ateline New World monkeys (Harrison, 1982; Strasser, 1988). Platyrrhines are proposed as most representative of the primitive condition, with cercopithecoids (along with atelids and great apes) being more derived. The great apes and atelids show greatest wedging and moderate asymmetry, whilst cercopithecoids have moderate wedging and marked asymmetry (Strasser, 1988). Both of these characters are suggested to be adaptive

for increased abduction during dorsiflexion. The taxa exhibiting a more primitive pattern are also characterised by locomotor repertoires that necessitate a considerable mobility in the ankle (particularly the pithecines who frequently utilise pedal suspension, and the hylobatids) and it seems likely that a high degree of flexibility, although possibly achieved in different ways, would constitute the primitive condition, and the increased stability of the cercopithecoids would consequently be derived.

The subtalar joint is relatively constant in form and function across primates, despite variation in the prominence of different characteristics (Lewis, 1980b). The most notable differences are between the New and Old World anthropoids, predominantly in the orientation of the subtalar axis, formed by the direction of curvature of the two talocalcaneal articulations, and thus the type of movement facilitated (Langdon, 1986). Evidently, increased flexibility of this joint has been achieved in contrasting ways by the more suspensory taxa of the different continental radiations. More subtle differences were apparent, however, between the cercopithecoids and the hominoids, pertaining chiefly to the degree of secondary mobility (Langdon, 1986).

The concave posterior calcaneal articulation of the cercopithecoid talus shows the shortest relative facet length among anthropoids, in combination with the greatest depth of curvature (Langdon, 1986; Strasser, 1988). This suggests retention of joint stability and a restricted range of motion. The anterior facet is split into proximal and distal parts on either sides of the underside of the neck. These two anterior facets are set acutely to one another, with opposing orientations, particularly in the more terrestrial species, thus restricting movement capabilities (Langdon, 1986; Strasser, 1988)[27]. In the more arboreal colobines, however, the opposition of these facets is less marked. The axis of curvature of the subtalar joint in the cercopithecoids verges on perpendicular to the long axis of the foot, limiting auxiliary motion during inversion/eversion. This overall morphology is much as would be expected for palmigrade arboreal quadrupeds, where a narrow

[27] Lewis (1981) and Strasser (1988) both hold the separated anterior talocalcaneal articulation to be a derived trait, adaptive for maintenance of stability during locomotion. It is also found in some New World monkeys, but with less opposition of orientation.

range of inversion/eversion would be necessary. It must be noted, however, that all primates utilise a degree of arboreal activity, which implies that all possess the ability to place the feet at irregular positions on substrates to a certain extent (Langdon, 1986).

In contrast, the posterior calcaneal facet is relatively longest and widest in the great apes, perhaps correlating to the increased stresses incurred by their greater body size. The facet is also significantly shallower, creating a larger range of excursion in inversion/eversion. The axis of curvature lies more obliquely to the long axis of the foot in all of the great apes, facilitating lateral rotation of the foot in inverted postures. The anterior facet on the talus is retained as a smoothly curved single facet in hominoids. Flexibility at the subtalar joint is especially critical for the prehensile role of the foot in climbing genera as they manoeuvre between inclined substrates, although they need to retain a certain amount of stability, and thus joint robusticity, across a range of pedal positions (Lewis, 1980c; Gomberg, 1985; Langdon, 1986; Strasser, 1988)[28].

Again, the hylobatid subtalar articulations exhibits a combination of cercopithecoid and great ape features, with a more perpendicular axis of curvature and more sharply curved facets than the great apes, but retention of the single anterior articulation (Langdon, 1986). Lewis (1980b) interprets the hylobatid subtalar joint as representative of a primitive form, which suggests both the cercopithecoid and great ape morphologies to be derived towards stability and mobility respectively.

In the atelines, the curvature of the posterior articulation lies in a more perpendicular plane, but mobility is retained through anteromedial movement of the calcaneus during inversion. Consequently, these New World monkeys have a large range of plantar/dorsiflexion at this joint, which would be adaptive for the prehensile function of the foot in these genera. This condition is also seen, to a certain extent, in *Pongo* (Langdon, 1986).

---

[28] Although many studies regard great apes as fairly consistent in their subtalar morphology, Oxnard and Lisowski (1980) propose that the talocalcaneal articulations differ significantly between *Pongo* and the African apes.

In the aspects of the talar head and neck pertaining to mobility in the midtarsal joint, several features are distinct between monkeys and apes. Again, these features relate to their varying locomotor repertoires, although *Pongo* showed a certain amount of convergence on the condition found in atelines (Langdon, 1986). The hominoids, with the notable exception of *Pongo*, show a short overall talar head and neck length, probably reflecting robusticity for the accommodation of stresses incurred by large body size during climbing (Langdon, 1986). The neck is more medially orientated than in the other groups, which would be the most likely direction for forces throughout this type of locomotion. The longer, more gracile talar necks of *Pongo*, and indeed the atelines, are probably the result of the minimised stresses incurred on the neck during pedal suspension, and might increase excursion capabilities at this joint during pronation/supination (Langdon, 1986).

Conversely, the cercopithecoid talar neck is orientated more into the longitudinal axis of the foot, which reflects the primary direction of stress during quadrupedal running and leaping. Gebo (1992) proposes that a talar head and neck orientated approximately in line with the talar body (in combination with other features of the talocrural, subtalar and transverse tarsal joints) would be adaptive for increased mobility in primates using heel-elevated, semi-plantigrade foot postures[29].

The shape of the talar head is quite varied across taxa, although Langdon (1986) argues that this may not be hugely important in ascertaining joint mobility. The

---

[29] Gebo (1992) argues that the fundamental differences between the tarsus of African apes and the other primate genera (except *Pongo*, which is unique) are due to the differing foot postures utilised during locomotor and postural behaviours. *Pan* and *Gorilla* habitually use plantigrade positions, where the heel strikes the substrate at the end of the swing phase of hindlimb movement. The primitive condition seen in all other primates is one of semi-plantigrade heel-elevated foot postures. The author hypothesises that this adaptation in African apes is an adaptation for long-armed quadrupeds to a more terrestrial lifestyle, and is fundamental to the origins of hominid bipedalism. This argument is strongly contested by Meldrum (1993; and also Schmitt and Larson, 1995), who suggests that plantigrady is seen in many primates and other mammals that frequently use slow, deliberate quadrupedalism, both on the ground and in an arboreal environment, whilst heel-elevated postures are most frequent during rapid running and leaping. Most interestingly, Meldrum suggests that this posture is used by atelines, suggesting that this could be a posture linked to climbing or suspensory behaviour, convergent in hominoids and atelines.

congruency of this aspect of the midtarsal joint is contingent on the shape of both the talar head, and the calcaneal and navicular articulations, as the talar head effectively locks into a socket formed by the facets on these two bones. Consequently it becomes difficult to determine the joint mobility without regarding all of the components simultaneously. In general, however, the hominoids, excepting *Pongo*, display a broad head, and the overall close-fitting of the joint is markedly less among hominoids than all other non-human anthropoids, resulting in a greater range of mobility at this joint than in the other taxa (Langdon, 1986).

In conclusion, there are only a small number of functional aspects of the talocrural joint that differ between hominoids and the other primates, other than those details of trochlear shape indicative of greater mobility and a less restrictive joint articulation (Langdon, 1986). It might be proposed that these are, however, fundamental in themselves due to the different requirements of the varying locomotor types for flexibility at this point. The subtalar joint, on the other hand, shows basic differences that pertain to both joint mobility and orientation, primarily in the structure of the facets and their angles of curvature. In the midtarsal joint, the primary differences can be related to the direction and magnitude of stresses during locomotion (Langdon, 1986).

The different specialisations observed in the extant taxa (Table 3) appear to be functionally related to role of the foot in their widely varying locomotor repertoires. In cercopithecoids, the foot is utilised predominantly for propulsion and balance, requiring overall stability within a conservative range of mobility, chiefly that of plantar and dorsiflexion. On the other hand, the more suspensory or climbing taxa regularly use their feet for support and/or hanging, and thus require greater capacity for strength in the feet, and greater grasping capabilities over a wide range of orientations. *Hylobates*, although perhaps the most specialised suspensory primate, is somewhat intermediate in its adaptations, combining derived hominoid traits with those of quadrupedal monkeys. Indeed, much of the evidence suggests that *Hylobates* retains a comparatively primitive morphology of the foot with respect to those seen in cercopithecoids and great apes. This is

probably due to the limited specialised pedal component in the locomotion of this genus.

	Atelines	Cercopithecoids	Hylobatids	*Pongo*	African apes	*Homo*
Talocrural joint						
Trochlear						
Breadth	wider	wide	narrowest	wider	narrow	widest
Arch height	lowest	high	high	high	flattens medially	low
Arc angle	less	greater	greater	less	less	less
Asymmetry	low	high	low	moderate	moderate	low
Wedging	high	low	low	low	moderate to high	low
Depth	variable	deep	shallow	deep	shallow	shallow
Subtalar joint						
Posterior facet						
Shape	long, narrow	short, wide	moderate length, broad	long, broad	long, broad	long, broad
Depth	shallow	deep	shallow	shallowest	shallow	shallow
Orientation	a-p	oblique	oblique	oblique	oblique	most oblique
Anterior facet curvature	less	extreme	some	less	least	most
Joint congruency	poor	moderate	good	least	moderate	moderate
Motion	mostly a-p, no screw action	slight rotation in place, slight screw action	rotation, slight screw action	rotation, screw action	rotation, screw action	mostly inversion/eversion, slight screw action
Talar positioning	centred on calcaneus	medial, little tilt	medial, little tilt	most medial, much tilt	most medial, much tilt	most centred
Mid tarsal joint						
Talar neck angle	slightly greater	slightly less	slightly greater	slightly greater	slightly greater	slightly less
Talar neck length	long	moderate	short	long	short	short
Talar head size	small	moderate	large	small	large	large

Table 3: Summary of osteological variation of the talar joints among extant anthropoids [after Langdon, 1986]

The African apes are quite primitive in their tarsal morphology, in contrast to the highly specialised *Pongo*, which is unique among the great apes in many aspects of its tarsal structure (Langdon, 1986). This may be attributed to the 'unique niche' occupied by this genus, incorporating a high degree of arboreal quadrumanous suspension despite large body size (Langdon, 1986). Indeed,

Meldrum (1993) proposes that *Pongo* has undergone a reversal from a terrestrial great ape ancestry, towards extreme arboreal behaviour (see also Smith and Pilbeam, 1980).

THE LORISID WRIST AND ANKLE JOINTS

In an analysis of the ulnocarpal articulations of Galagidae and Lorisidae, Cartmill and Milton (1977) observed fundamental differences between the two lorisoid families pertaining to joint mobility. Firstly, the galagid pisiform is of the primitive mammalian configuration, elongated and projecting back to form the 'heel' of the hand, with a clear facet for direct articulation with the ulna. The loris pisiform, on the other hand, is relatively small, distally displaced and separated from the ulna by radiolucent tissues. Secondly, the galagid ulnotriquetral joint shows clear direct articulation with the pisiform and triquetral forming a cup-like socket for reception of the short, stout distal ulna. In lorises, the triquetrum and ulna are separated by a considerable gap. The ulna styloid process is a relatively slender projection, with a somewhat small articular surface on its distal extremity. Finally, the galagid distal radioulnar articulation is relatively small and flat, compared to that of the lorises. The articular portion of the loris distal radius extends across towards the ulna styloid process, inserting itself between the ulna shaft and the carpus. On the whole, the loris radioulnar articulation is characterised by expansion of the articular surfaces on both the radius and ulna, suggesting a greater range of excursion of the radius around the ulna.

Overall, the galagid ulnocarpal joint is uniformly observed to be of the primitive mammalian type, with the large distal end of the ulna styloid process articulating directly with the receptive cup formed by the triquetral and pisiform. In contrast, the lorisids show various degrees of ulna withdrawal from the carpus, across the three genera examined. In *Loris*, the ulnocarpal joint is much reduced, with the distally displaced pisiform articulating solely with the triquetrum. The ulna exhibits a slender styloid process with a small articular surface at its terminus, which only contacts the triquetrum during ulna deviation and dorsiflexion of the hand. Cartmill and Milton (1977) suggest that this contact does not appear to restrict ulnar deviation of the hand. The radioulnar joint is fully diarthrodial.

Perodicticus is slightly more advanced in the withdrawal of the ulna from the carpus. Like *Loris*, a fibrous ridge intercedes between the triquetrum and ulna styloid process, although limited stylotriquetral contact is retained. Again, no articulation is evident between the pisiform and the ulna styloid process. Although these fundamental features are similarly observed in *Nycticebus*, this genus shows great variation in its degree of ulnotriquetral contact across specimens, ranging from direct contact between the ulna and triquetral to complete exclusion of the triquetral from the ulna by the presence of intra-articular fatty pad.

On the whole, the two lorisoid families are observed to have very different structures of the ulnocarpal joint from one another, which probably reflects the demands presented by their widely contrasting locomotor and postural repertoires. The galagid wrist resembles the primitive arrangement seen in other mammals, and thus we can assume that it is the lorises that have become derived in this element of their anatomy. Evidently the lorises have acquired these features in response to the adaptive pressures of their environment and habits. Cartmill and Milton (1977: 260) note that these derivations of the loris wrist were essentially of the same nature as those documented by Lewis (1971a, 1972a-b, 1974) in his many papers on the hominoid wrist: "The observations presented here show that the wrist of lorisines (and of some *Nycticebus* in particular) is not typically mammalian, but has undergone a transformation as radical as, and in many respects parallel to, that seen in the extant Hominoidea".

Furthermore, lorisids exhibit other characters of the postcrania that might be seen as convergent on hominoid locomotor anatomy, including relatively high intermembral indices, features of the shoulder joint pertaining to increased overall mobility (moderate cranial orientation of the glenoid fossa, elongated of scapula vertebral border), features of the torso (transverse breadth of the thoracic cage exceeds dorso-ventral breadth), and a reduced tail (Cartmill and Milton, 1977; see also Runestad, 1997 for features pertaining to limb mobility). It is not unreasonable to suppose that these similarities indicate a comparable functional role. These features, however, have traditionally been associated with brachiating locomotion, and their presence in the non-brachiating lorisids poses a challenge to that inference.

The lorisid wrist modifications can be functionally attributed to their characteristic locomotor pattern, which incorporates slow climbing, cautious quadrupedalism, hindlimb suspension, quadrumanous below-branch activity and bridging behaviours, and necessitates a high degree of postcranial flexibility for reaching and hauling the body (Cartmill and Milton, 1977). The ulna retreat from the carpus facilitates increased excursion of the wrist in the rotation of the hand about the longitudinal and dorsoventral axes, for pronation/supination and abduction/adduction respectively. As a result, lorisids are well equipped for gripping substrates in a variety of postures. Similar wrist adaptations have also been noted in the two-toed sloth, which engages in comparable postural and locomotor activities (Cartmill and Milton, 1977).

Thus, parallel adaptations seen in the hominoids and lorisids might imply that the apes experienced a phase of cautious quadrupedalism before the emergence of the locomotor specialisations seen in apes today (Cartmill and Milton, 1977). Large arboreal animals are less likely to employ leaping or jumping behaviours, due to their considerable body weight, and thus might utilize hoisting, reaching and bridging to negotiate between arboreal supports. These taxa would also have a greater need to evenly distribute their weight across supports, which would be assisted by grasping ability throughout a range of postures. Additionally, genera engaging in this cautious form of locomotion would have less need of a tail, as the tail is effectively a balancing agent for many arboreal species, and may be used to radiate the excess heat energy incurred though rapid arboreal activity (Cartmill and Milton, 1977).

Analyses of the ankle and foot of lorisids have also observed osteological features that fundamentally pertain to the increased prehensile function of the foot in these taxa during their extraordinary 'sloth-like' climbing behaviour (Grand, 1967). In his study of four lorisid genera (*Nycticebus*, *Loris*, *Perodicticus*, and *Arctocebus*), Grand (1967) observed that the prehensile function of the foot played a far more important role than the propulsive function during lorisid locomotion. This increased prehensility is facilitated by a three joint action in the ankle, whereby plantarflexion, inversion and flexion are carried out simultaneously at the

talocrural, subtalar and midtarsal joints respectively. During climbing the talocrural joint is predominantly engaged in plantarflexion, and the subtalar joint inverted, with additional flexion noted at the midtarsal joint for extra grasping (Grand, 1967).

The lorisid talocrural joint, like that of other primates, comprises the articulation of the talus with the distal extremities of the lower leg bones, whereby the talus is securely locked beneath the tibia and fibula during inversion/ eversion; contact is maintained between the medial, lateral and superior aspects of the talus and the tibial and fibular malleoli. The hinge like mechanism of the joint permits plantar/dorsiflexion across a range of about 100° of motion. The ligaments of the joint assist in retaining the single plane of motion in this joint (Grand, 1967).

The subtalar joint consists of two articular facets, jointly contributing to a single axis of movement. As the talus is tightly bound, allowing restricted mediolateral excursion, the calcaneus, navicular and distal foot move relative to the talus, at the subtalar joint, to contribute to the range of mobility. These movements take place at the posterior and anterior talocalcaneal articulations, and at the transverse tarsal joint. The primary direction of motion at these points is inversion/eversion. The navicular articulates mediolaterally with the anterior surface of the flattened talar head, facilitating inversion/eversion across a range of approximately 60-70° (Grand, 1967). Additional inversion and flexion also occurs at the metatarsals and digits. This inverted posture of the foot, accompanied by plantarflexion at the talocrural joint, is documented as the natural position of the tarsus and digits relative to the ankle (Grand, 1967).

Overall, the lorisids have an exceptionally prehensile foot, which appears functionally adapted to their distinctive locomotor pattern. These adaptations have occurred at the talocrural, subtalar and midtarsal joints, to provide a pivot for the foot to grasp in a multitude of orientations. Although Grand's (1967) paper does not address the relationship directly, it can be inferred that the structure of the lorisid ankle is somewhat different from that seen in extant hominoids, given that the hominoid talus is less rigidly secured at the talocrural joint, offering a greater

range of mediolateral mobility (Langdon, 1986). It might be deduced that the talar trochlea exhibits limited wedging in lorises, as there is little accessory motion across the range of postures. The report, however, does imply similar extent of mobility at the subtalar joint, contributing to the overall movement capabilities of the foot. This may be evident in similarities of structure that are not examined in the article, although the paper (Grand, 1967) does suggest a hominoid resemblance in the shape of the talar head.

In view of the implied morphological similarities between the lorisid and hominoid wrist, and their implications for potential underlying postural/locomotor repertoires (Cartmill and Milton, 1977), and the comparable movement capabilities evident in certain aspects of the ankle in these taxa, it might be logical to expect certain parallelisms in aspects of ankle morphology as well.

THE EARLY MIOCENE HOMINOID WRIST

Studies of the proconsulid wrist joint have varied considerably in their results, and subsequent interpretations of early Miocene ape locomotion. In the earliest literature *Dryopithecus (Proconsul) africanus* (now assigned to *Proconsul heseloni* [Walker et al., 1993]) was widely accepted to possess primitive wrist morphology, consistent with that of an arboreal quadruped (Napier and Davis, 1959), although Lewis (1972a) argued that these fossil descriptions were generally carried out before the knowledge of unique hominoid wrist adaptations.

There has been much debate as to the significance of features observed in the ulna and carpus of the early Miocene taxa, and indeed the different analyses have been somewhat contradictory in their descriptions of the same specimen. Some analyses have described incipient hominoid features of the wrist (Lewis, 1971a; Beard et al., 1986; Odhiambo Nengo and Rae, 1992), and others have noted more monkey-like characteristics (Schon and Ziemer, 1973; Corruccini et al., 1976; Morbeck, 1975; Harrison, 1982).

The ulna styloid process in the *P. heseloni* (KNM-RU 2036[30]) specimen is relatively longer than all extant anthropoids, verging on the morphology found in strepsirhines (Harrison, 1982), and has variously been described as hook-like (Lewis, 1971a, 1972a-b) or robust (probably weight-bearing) and not hook-like (Morbeck, 1975). Harrison (1982) suggests, however, that the reported length of this specimen might be attributed to either its juvenile status, or measuring difficulties encountered due to fossil damage. This specimen has well-defined articular surfaces on the distal and peripheral aspects, dorsolaterally placed rather than on the carpal aspect as found in extant monkeys (Lewis, 1971a; Morbeck, 1975). This articulation, however, comprises a distinct oval facet for the triquetral, with a less clear elongated depression on the periphery for the pisiform (Morbeck, 1975). This would suggest that the ulna styloid process of this specimen retained a significant articulation with the carpus, unlike the hominoids where this contact is reduced. In addition, the distal radioulnar and radiocarpal articulations suggest limited pronation-supination and radial-ulnar deviation (Morbeck, 1975). On the other hand, the orientation of the carpal facets is reflective of a hominoid-like reorganisation of the joint (Lewis, 1971b).

Analyses of other specimens from the early Miocene have found that some of the fossils (KNM SO 1012 and KNM CA 575, assigned to *Dendropithecus macinnesi* and *Kalepithecus songhorensis*[31], respectively) most closely resemble cercopithecoid monkeys in the structure of the distal ulna (Harrison, 1982) whilst a specimen assigned to *P. major* is more hominoid-like (Odhiambo Nengo and Rae, 1992). The *Dendropithecus* and *Kalepithecus* specimens possess relatively long ulna styloid processes, comparable to non-hominoid anthropoids, with clear facets for the pisiform and triquetral. They also exhibit an anteroposteriorly long and narrow head, and a radial articulation suggestive of limited excursion (Harrison, 1982). This is in contrast to specimen KNM-SO 22734, a distal fragment of an ulna, which is tentatively assigned to *P. major* on the basis of size (Odhiambo Nengo and Rae, 1992). The specimen, consisting of the ulna head and

---

[30] One of the difficulties with the analysis of this particular specimen is that it is a juvenile, and any study must take into consideration the ontologenetic differences that might be apparent between this and adult specimens (see Harrison, 1982).

[31] Originally referred to *Micropithecus songhorensis* (Harrison, 1982), but assigned to *Kalepithecus songhorensis* by Harrison (1988).

a tiny portion of the styloid process, is most similar to living hominoids in the morphology of the ulna head, but different to *P. africanus*. "The large articular facet suggests an animal capable of a range of wrist mobility similar to that of *Pan troglodytes*" (Odhiambo Nengo and Rae, 1992: 427).

The long ulna styloid processes observed in some of the above specimens, in combination with the other characters, imply limited wrist mobility (particularly abduction-adduction) reminiscent of that seen in cercopithecoids (Harrison, 1982, 1987). It seems that *P. heseloni*, *D. macinnesi* and *K. songhorensis* retain features of the ulna more consistent with the primitive catarrhine pattern (large and well-developed ulna styloid process, direct contact between the ulna styloid process and the carpus, no intra-articular meniscus, restricted radioulnar articulation, and anterior-posteriorly long and narrow distal ulna), differing from extant hominoids in these aspects. The wrist of these specimens is thus not similar in its articular surfaces and reconstruction of movement capabilities to extant hominoids, but more like palmigrade, quadrupedal cercopithecoids (Morbeck, 1975; Harrison, 1982, 1987). In contrast, *P. major* shows features of the radioulnar articulation reminiscent of greater mediolateral excursion and thus greater potential for mobility of the wrist (Odhiambo Nengo and Rae, 1992)

Morbeck (1975) suggests that the size and shape of the pisiform, and the placement of the articular facets on the ulna, triquetral and pisiform are most consistent with habitual palmigrade locomotor behaviour, and infers the range of motion to be most similar to palmigrade quadrupeds[32]. Several analyses of the wrist of *P. heseloni* and *P. nyanzae* have, however, shown that the carpal anatomy of *Proconsul* shows structural similarities to extant hominoids, but in combination with characteristics similar to cercopithecoids (Lewis, 1971a; Beard et al., 1986). The pisiform and triquetrum of both fossil species show clear articular facets for the ulna styloid process, like extant monkeys, but the orientation of the articular

[32] Morbeck (1975), however, recognises the speculative nature of interpretation/reconstruction of locomotor/positional behaviour in view of the fragmentary/damaged nature of much of the material and the limited samples available for many of the species. In addition, she highlights the problems of working with cast material, where subtle details of the anatomy of joint surfaces may be obscured (see also Ford, 1988 for problems of reconstructing the behaviour of fossil taxa from comparative analyses with extant forms).

surfaces differs from cercopithecoids, suggesting different movement capabilities to extant taxa (Lewis, 1971a; Beard et al., 1986). The triquetral has the appearance of a triangular pyramid, the palmar surface of which has a large, shallowly concave facet for pisiform (Lewis, 1971a). The pisiform has a large dorsal facet for the triquetral, and a smaller meniscal facet on its proximal aspect, with some evidence for the division of the articular area (articular at the tip for the triquetral, and the periphery area for the meniscus) (Lewis, 1971a). This suite of characters is suggestive of a meniscus-containing joint, and the subsequent orientation of the triquetral and pisiform indicates a more hominoid-like organisation of the ulnocarpal joint (Lewis, 1971a).

The presence of ulnocarpal articulation restricts the degree of ulnar deviation characteristic of extant hominoids, and therefore supination of the forearm must have been more limited in *Proconsul*. But the extent and orientation of ulnocarpal articulation was different from that of cercopithecoids (Beard et al., 1986). Despite articulation with the carpus the *Proconsul* ulna styloid process would have had a greater extent of distomedial displacement on the pisiform and triquetral than extant monkeys. Also, the proximodistal (rather than mediolateral) orientation of the spiral facet on the hamate would have facilitated ulna deviation further. *Proconsul*, therefore, shows derived characters for catarrhines, but is not equivalent to modern hominoids (Beard et al., 1986). In this sense, *Proconsul* is unique, and is not matched by extant species. "The wrist of *Proconsul* may have been subjected to some of the same selective forces which eventually brought about the reorganisation of the modern hominoid wrist" (Beard et al; 1986: 117), which is consistent with this genus constituting a basal member of the hominoid group.

Overall there has been a significant amount of disagreement with regard to the interpretation of features of the proconsulid distal ulna and carpus. Analyses have identified characters reminiscent of both extant hominoids and cercopithecoids, and it seems likely, as has been shown with the rest of the early hominoid postcrania, that these taxa possessed a suite of characteristics unmatched by extant taxa. There is no evidence to support the suggestion proposed by Conroy and Fleagle (1972) and Zwell and Conroy (1973) that the wrist of *Proconsul* shows

adaptations to the specialised knuckle-walking form of locomotion characteristic of modern African apes (based on Tuttle's 1967 list of characters) (Morbeck, 1975; Beard et al., 1986). The presence of these features pertaining to increased supination has been interpreted as suggestive of adaptations towards suspensory locomotion and posture being already well established in the early Miocene Hominoidea (Lewis, 1971a; 1972a-b, 1974). Although increased supination can be related to brachiating capabilities, the relationship is not exclusive, and authorities agree that the ulna and carpus of the early Miocene taxa were not adapted to specialised brachiating locomotion (Beard et al., 1986). Accordingly, the locomotor patterns utilised by these genera were probably rather different from those seen in any of the modern anthropoids. The configuration of the wrist allowed a greater range of mobility than seen in extant cercopithecoids, but in combination with a greater degree of stability than hominoids, as might be expected for a pronograde quadruped engaging in four-limbed grasping quadrupedalism.

THE EARLY MIOCENE HOMINOID ANKLE

A great many studies have been undertaken to compare fossil tali with those of extant genera, because of the crucial position of this bone in connecting the foot to the ankle and thus its importance in determining the function of the foot as a whole. In addition, there are a significant number of tali preserved in the fossil record from this period, from a wide range of early Miocene genera (Lisowski et al., 1974).

In a similar way to studies of the wrist, comparisons of the morphological features of the ankle (talocrural and subtalar joints) in early Miocene forms have yielded a wide range of results, finding affinities of the different genera with hylobatids (Lisowski et al., 1976), *Pongo* (Lisowski et al., 1974, 1976), modern great apes (Day and Wood, 1969; Pilbeam, 1969), Old and/or New World monkeys (Corruccini et al., 1976; Le Gros Clark, 1952; Le Gros Clark and Leakey, 1951; Preuschoft, 1973; Wood, 1973, Harrison, 1982), or, most recently, a combination of monkey- and ape-like characteristics (Langdon, 1985, 1986; Ward, 1997).

Specimens of *Proconsul* and *Rangwapithecus* have revealed remarkable similarity in their features, despite size differences (Harrison, 1982), although the smaller *Proconsul africanus* (including material now assigned to *P. heseloni*) and *Rangwapithecus gordoni* show sharper trochlear curvature (deep and asymmetrical), than the larger *P. nyanzae* and *P. major* (Langdon, 1986).

At the talocrural joint, *Proconsul* and *Rangwapithecus* are similar in their shape and curvature to African apes, but resemble monkeys in specific features suggesting restricted mediolateral mobility (Langdon, 1985; 1986). All of the specimens have relatively deeply grooved trochlea surfaces, and slight anteroposterior wedging, equivalent to or less than that seen in extant cebids and cercopithecines. The fossil tali also exhibit steep malleolar facets, and well-defined medial and lateral crests, with moderate asymmetry comparable with Asian apes and colobine monkeys (Harrison, 1982; Langdon, 1986). These features contrast with the condition found in African apes (a shallow trochlea with ill-defined crests) that allows greater accessory movement at this joint (Harrison, 1982). In summary, mobility at the talocrural joint in the fossil taxa is fairly restricted (Langdon, 1986), and most like cercopithecoids in features pertaining to the stability of talocrural joint (deep trochlea groove, angular crests,), but in aspects of the medial and lateral tubercles, trochlear wedging and degree of asymmetry, they correspond most closely to arboreal non-catarrhine primates (Harrison, 1982). Ward (1997) suggests that these fossil taxa have a primitive talocrural joint, indicative of palmigrade quadrupedalism.

Conversely, the subtalar and midtarsal joints are more similar to great apes, with enlarged talocalcaneal articular surfaces (expanded anteromedially) offering a wider range of mobility at this point (Langdon, 1986)[33], although Harrison (1982) disputes this in recommending the total subtalar structure to be reflective of arboreal quadrupedalism. Ward (1997) noted that the orientation and structure of the talar articular facets on the calcaneus are more comparable to extant colobines, resulting in an intermediate range of mobility at the subtalar joint.

---

[33] This is similar to the observations documented in Grand (1967) on the structure of the lorisid ankle, with restricted talocrural morphology, and enhanced mobility at the subtalar and midtarsal joints.

The fossil tali have short necks and well rounded heads, similar to the great apes[34] (Langdon, 1986), and in the orientation of the head and neck, and the inclination of the subtalar joints, the structure suggest a prehensile and opposable hallux (Harrison, 1982). Moreover, the midtarsal joints and tarsal lengths are most like those of extant hominoids (Ward, 1997). Harrison (1982: 416) concludes that overall analysis shows the fossil apes to be arboreal quadrupeds, but states "the combination of morphological features seen in the fossils distinguishes them from all extant catarrhines, and probably represents a structurally less specialised grade of development associated with generalised arboreal activities".

Both *Proconsul* and *Rangwapithecus* possess features of the talus, calcaneus, and the proximal anterior tarsal joints that indicate ape-like slow-climbing, positional and locomotor capabilities, but with restricted mediolateral displacement at the talocrural joint. Langdon (1986: 173) states, "The *Proconsul* foot appears to be capable of both vertical climbing postures and limited monkey-like progression."

The talus of *Dendropithecus* reveals no characteristics that would indicate different positional repertoires from those of *Proconsul*, but the calcaneus shows greater similarity to great apes and atelines, with overall gracility indicating more suspensory functions (Langdon, 1986). *Micropithecus*, *Kalepithecus*, and (to a lesser extent) *Limnopithecus legetet*, have longer talar necks than the other species, comparable with those of the suspensory atelines, but most elements of the talocrural and subtalar joints are functionally indistinguishable from *Proconsul* (Harrison, 1982; Langdon, 1986).

Overall, the ankle and foot morphology of Miocene apes is quite generalised in comparison to extant forms (Ward, 1997). The fossil taxa reveal a mosaic of traits unlike living primates, with features indicative of quadrupedalism forming the primary mode of locomotion (stability at the talocrural joint, restricted to plantar/dorsiflexion, and gracile, and elongated, anterior tarsal skeleton)

---

[34] A short talar neck and head is identified as a hominoid synapomorphy by some authors (e.g., Rae, 1999), although Langdon (1986) argues that *Pongo* is an exception to this, having an elongated narrow neck similar to that found in the atelines.

(Harrison, 1982; Langdon, 1986; Ward, 1997). In combination with this, these early species possess features functionally correlated with increased climbing: increased subtalar and midtarsal mobility, and a strongly developed grasping hallux. These species, and particularly the best-known *Proconsul*, probably incorporated both climbing and quadrupedalism in their locomotor repertoires, although most likely at slower speeds than extant monkeys, due to the robusticity of their postcranial skeletons (Langdon, 1985, 1986).

CHAPTER 4

Aims and Objectives

There is little doubt, from the review of the previous literature documenting the postcrania of early hominoids, that the early Miocene genera were very different from the extant hominoids in both their morphology and inferred locomotor repertoires. These taxa were fundamentally monkey-like in their axial skeleton, and thus primarily adapted for pronograde arboreal quadrupedalism (Ward, 1993a-b). Nevertheless, the high range of mobility in most of the joints of the appendicular skeleton suggests a greater range of movement than modern monkeys (e.g., Fleagle, 1983; Rose, 1983; MacLatchy and Bossert, 1996). Indeed most authorities agree that the postcranial evidence supports a view that these genera were rather slow, but powerful, arboreal climbers, utilising strong pedal and manual grasping (e.g., Begun et al., 1994; Rose, 1997).

If we accept the proconsulids as hominoids, three of the previous hypotheses postulated for the ancestral hominoid locomotor pattern (brachiation, knucklewalking and vertical climbing) can more or less be falsified on the basis of the fossil data, in combination with observations from extant forms. The early Miocene hominoids show none of the specialisations indicative of brachiating behaviours, and the extant great apes do not use this type of behaviour frequently (Fleagle et al., 1981). Indeed only the hylobatids regularly use ricochetal arm-swinging locomotion, and they are characterised by the least derived morphology in the traits usually associated with brachiation (Conroy and Fleagle, 1972). Similarly the Miocene forms show none of the specialisations expected for knucklewalking (Morbeck, 1975; McHenry and Corruccini, 1983), and it is only the African apes that use this form of quadrupedalism. It is probably realistic, however, to agree that both of these aforementioned locomotor types are derived specialisations from a common ancestral base (Langdon, 1986). With reference to the vertical climbing hypothesis, whilst the Miocene forms seem well adapted in their appendicular skeleton to this type of locomotion, the primitive nature of the

axial skeleton suggests that these forms were fundamentally pronograde (Ward, 1993a). Additionally, extant taxa do not show frequent vertical climbing behaviour, and this form of locomotion would have to include other behaviours as well, as vertical climbing is only practised 'up and down' (Gebo, 1996).

This leaves us with the cautious quadrupedalism hypothesis. The suggested resemblances between the hominoid and lorisid wrist joint (Cartmill and Milton, 1977) imply a similar functional adaptation. The lorisids are characterised by their slow, deliberate quadrupedal progression, which requires a considerable range of mobility of the limbs, most particularly the hands and feet, to accommodate grasping irregular arboreal supports in a multitude of orientations (Walker, 1969; Cartmill and Milton, 1977; Grand, 1967). A loris locomotor type would account for all of the features found in the early Miocene genera; monkey-like axial skeleton, enhanced mobility in the limbs, powerful grasping capabilities, and loss of tail (Kelley, 1997). Furthermore, this form of locomotion would provide a reasonable base from which the more specialised extant hominoid locomotor patterns could have evolved (Kelley, 1997).

Unfortunately, apart from the study by Cartmill and Milton (1977), which suggested similarities between the wrists of lorisids and hominoids, there is limited comparative data on these taxa, and more particularly with the fossil taxa. It is therefore necessary to test whether these groups share any other postcranial features that might further support this hypothesis. One of the fundamental adaptations to this form of locomotion would be greater mobility of the ankle joint, and the hominoids are known to possess derived ankle morphology (Langdon, 1986). If the lorisids are shown to have similar adaptations in this anatomical region to the hominoids, as well as in the wrist, it would support the hypothesis of the original hominoid postcranial adaptation being one of loris-like locomotor capabilities. Thus, this study is a continuation from that of Cartmill and Milton (1977) in that it conducts a direct comparison of wrist and ankle features of lorisids, hominoids and proconsulids across a range of characters.

The aim of this study, therefore, is to examine features of the talocrural, subtalar and midtarsal ankle joints and the ulnocarpal and radioulnar joints in the wrist that

relate to the range of mobility in these structures. The characters reviewed in this study are ulna styloid process length, extent of ulnocarpal articulation, ulna head shape, shape and extent of the radioulnar articulation, talar trochlear depth, extent of anteroposterior trochlear wedging, depth of curvature of the posterior calcaneal facet, obliquity of the subtalar axis, talar head breadth, and length and orientation of the talar head and neck. These characters are studied across a spectrum of primates, chosen to reflect a range of arboreal quadrupeds and suspensory forms, to provide adequate comparative material with which to test hypotheses of the relationship of form to function. The view is to compare the anatomy of lorisid and hominoid taxa within a context of other, tailed, arboreal quadrupeds. This study predicts that the lorisids are similar to the hominoids in these features, from which it may be inferred that the traits reflect similar functional adaptations. The data will then be compared with the same features in the Miocene taxa to test hypotheses of ancestral hominoid patterns.

CHAPTER 5

Methods and Materials

NEONTOLOGICAL SPECIMENS

The data are derived from original observations and measurements of primate specimens from the collections at the American Museum of Natural History in New York (AMNH) and the National Museum of Natural History at the Smithsonian Institute in Washington DC (NMNH). A total of two hundred and twenty-nine specimens were analysed, representing fourteen genera: *Arctocebus*, *Nycticebus, Loris, Perodicticus, Varecia, Alouatta, Saimiri, Chiropotes, Cercopithecus, Macaca, Hylobates, Pongo, Pan* and *Gorilla* (Table 4). The primary focus of the study was analysis of the hominoids and lorises, and thus data sets were collected for all genera within these groups. The remaining taxa were chosen to reflect arboreal quadrupeds of varied body size across the spectrum of taxonomic groupings.

Where possible, data for 20 specimens from each of the taxa was obtained; the samples studied for some of the genera (*Arctocebus*, *Loris*, *Nycticebus*, *Varecia*, and *Chiropotes*) were restricted by the numbers of specimens within the museum collections. All specimens were adult, wildshot, with no apparent deformities through illness or injury. Every effort was made to collect equal numbers of males and females. In some cases, however, sex was indeterminate and in others the limitations of the collections did not allow for such choice.

FOSSIL SPECIMENS

The fossil data used in this study derived from previous studies of the ulna and talus of Miocene hominoids (Table 5). Only a few of the wrist measurements could be achieved from the literature, and these were taken from Harrison (1982). As a result, the only indices that could be meaningfully compared with the extant data for the wrist were those of ulna styloid process length and ulna head shape.

The distal ulna specimens for which data were available represented two species: *Proconsul heseloni* and *Kalepithecus songhorensis.*

Genus	Males	Females	Indeterminate	Total
Lorisidae				
Arctocebus	1	1	1	3
Loris	3	0	2	5
Nycticebus	3	3	8	14
Perodicticus	11	8	3	22
Lemuridae				
Varecia	2	5	2	9
Atelidae				
Alouatta	9	11	5	25
Chiropotes	2	5	0	7
Cebidae				
Saimiri	8	13	2	23
Cercopithecidae				
Cercopithecus	11	8	1	20
Macaca	11	8	1	20
Hylobatidae				
Hylobates	8	9	3	20
Great apes				
Gorilla	10	4	11	25
Pan	7	7	6	20
Pongo	6	9	5	20

Table 4: Summary of osteological samples

The data for the Miocene tali were available for most of the measurements used in this study, and for a larger sample of species than those of the wrist. These figures were derived from the original data used by Langdon (1984), conveyed by personal communication, and from Harrison (1982). The sample included: *P. africanus*, *P. major*, *P. nyanzae*, *P. heseloni*, *D. macinnesi*, *R. gordoni*, *K. songhorensis*, *L. evansi*, and *L. legetet.*

Number	Specimen	Locality	Species
Ulna			
KNM-RU 2036	L distal ulna	Rusinga	*P. heseloni*
KNM-CA 575	R distal ulna	Chamtwara	*K. songhorensis*
KNM-SO 1012	L distal ulna	Songhor	*K. songhorensis*
Talus			
KNM-RU 4347	R talus	Rusinga	*P. africanus*
KNM-RU 1744	L talus	Rusinga	*P. africanus*
KNM-RU 1745	R talus	Rusinga	*P. africanus*
KNM-SO 1402	R talus	Songhor	*P. africanus*
KNM-SO 389	R talus	Songhor	*P. major*
KNM-SO 1705	L talus	Songhor	*P. major*
KNM-RU 1743	L talus	Rusinga	*P. nyanzae*
KNM-RU 1896	L talus	Rusinga	*P. nyanzae*
KNM-RU 3105	R talus	Rusinga	*P.nyanzae*
KNM-RU 2036	L talus (juvenile)	Rusinga	*P. heseloni*
KNM-RU 1748	L talus	Rusinga	*D. macinnesi*
KNM-RU 1663	R talus	Rusinga	*D. macinnesi*
KNM-SO 966	L talus	Songhor	*R. gordoni*
KNM-SO 968	R talus	Songhor	*R. gordoni*
BM(NH)-M 26309	R talus	Songhor ?	*R. gordoni*
KNM-SO 478	L talus	Songhor	*K. songhorensis*
KNM-SO 967	L talus	Songhor	*K. songhorensis*
KNM-CA 1305	L talus	Chamtwara	*K. songhorensis*
KNM-SO 392	L talus	Songhor	*L. evansi*
KNM-LG 621	L talus	Legetet	*L. legetet*

Table 5: Miocene hominoids included in this analysis

MEASUREMENTS

In the present analysis of the wrist and ankle, measurements were taken from the talus and distal ulna, with additional comparative measurements from the ulna shaft. In some cases, the condition of the specimens did not allow for a complete data set and thus some statistics were derived from fewer individuals. Wherever possible measurements were taken from the right-hand side to ensure consistency.

A total of twenty-seven measurements were taken (Table 6). Linear measurements were taken using digital callipers (Mitutoyo 'Absolute Digimatic') in mm, to two decimal places, and angles were measured with a protractor to the nearest degree. The measurements of the ulna were calculated to provide relative length of the ulna styloid process, relative size of the ulnar triquetral facet, relative extent of the ulnar radial facet, ulnar head shape, and distal ulna shape. The measurements of the talus were calculated to discern relative depth of the talar trochlea, index of talar trochlea wedging, relative depth of the posterior calcaneal facet, the angle of the subtalar axis from the lateral crest, relative talar head breadth; and relative talar head and neck length. These results were then compared between the taxonomic groups. The angle of the talar head and neck projection was compared directly between the groups studied.

Ulnocarpal joint

The length of the ulna styloid process (USPL) was measured as the maximum projection of the process beyond the ulna head. This was measured with the depth gauge on the callipers from the distal tip of the process to the highest point on the ulna head. In some cases (most particularly in the hominoids), a distinct groove was present between the ulna styloid process and the part of the head bearing the articular facet for the radius. In these specimens two measurements were taken from which the ulna styloid projection was derived: the depth of the ulna styloid process from the base of the groove (USPD), and the height of the radial articulation on the head (UHD). UHD was then subtracted from USPD to calculate USPL.

The dimensions of the carpal facet on the ulna styloid process (UCF-ML and UCF-AP) were measured as a maximum mediolateral width and a transverse axis (orientated anteroposteriorly, proximodistally, or obliquely between these extremes).

Measurement	Description	Calculation
Ulna		
Ulnocarpal joint		
USPL	Ulna styloid process length	USPD – UHD
USPD	Ulna styloid process depth	
UHD	Ulna head depth	
UCF-ML	Ulnocarpal facet mediolateral breadth	
UCF-AP	Ulnocarpal facet anteroposterior length	
UCFA	Ulnocarpal facet area	UCF-ML . UCF-AP
Ulna mid-shaft		
UMS-AP	Ulna mid-shaft anteroposterior breadth	
UMS-ML	Ulna mid-shaft mediolateral breadth	
UMSA	Ulna mid-shaft cross-sectional area	UMS-AP . UMS-ML
Radioulnar joint		
UH-AP	Ulna head anteroposterior length	
UH-ML	Ulna head mediolateral breadth	
UHA	Ulna head cross-sectional area	UH-AP . UH-ML
URF-ML	Ulnoradial facet mediolateral breadth	
URF-PD	Ulnoradial facet proximodistal height	
Talus		
TL	Talus length	
Talocrural joint		
TTD	Talar trochlea depth	
TTB	Talar trochlea breadth	
TTL	Talar trochlea length	
TTAB	Talar trochlea anterior breadth	
TTPB	Talar trochlea posterior breadth	
Subtalar joint		
TPCFD	Talar posterior calcaneal facet depth	
TPCFL	Talar posterior calcaneal facet length	
ACPCF-LC	Angle of curvature of posterior calcaneal facet to lateral crest	
Talar head and neck		
THB	Talar head breadth	
THD	Talar head depth	
THNL	Talar head and neck length	TL – TTL
ATH-LC	Talar head angle from lateral crest	

Table 6: Measurements used in analysis

Ulna mid-shaft

These measurements were calculated by ascertaining the length of the ulna, and taking both the mediolateral (UMS-ML) and anteroposterior (UMS-AP) diameters at the mid-point.

Radioulnar joint

The dimensions of the ulna head were obtained in both anteroposterior (UH-AP) and mediolateral (UH-ML) directions, from the maximum points. The extent of the radial articular facet on the ulna head was taken primarily mediolaterally (URF-ML), but also proximodistally (URF-PD) to illustrate the shape of the facet. In cases where the facet extended around the ulna head, the index may not reflect the true range of radial excursion, as the measurement was linear.

Talocrural joint

The depth of the talar trochlea (TTD) was measured with the depth gauge on the callipers from the mid-point of the line connecting the most superior points on the medial and lateral crests. In the larger taxa (*Pongo*, *Pan* and *Gorilla*) this was achieved by placing a piece of wire across the two crests, measuring the depth and subtracting the diameter of the wire. The breadth of the trochlea (TTB) was measured across this line connecting the highest crest points. The anterior breadth (TTAB) was measured across the most direct line connecting the forward most points of the medial and lateral crests, and the posterior breadth (TTPB) was similarly taken across the most dorsal points of the crests. The length of the talar trochlea (TTL) was measured between the most dorsal and ventral points on the trochlea, along the longitudinal axis of the trochlea.

Subtalar joint

The depth of the posterior calcaneal facet (TPCFD) was measured with the depth gauge on the callipers, from the highest point of the extremities of the maximum length of the facet. Again, with the larger taxa, a strip of wire was placed across the length in order to measure the depth, and the wire diameter was subtracted for the result. The length of the facet (TPCFL) was taken as the maximum distance

between the facet extremities, parallel to the axis of curvature. The angle of curvature of the posterior calcaneal facet (ACTPCF) was taken by positioning the talar head on its superior aspect (trochlea facing down), with the lateral crest to the horizontal, and drawing the direction of curvature in relation to the horizontal. The angle was then measured from the diagrams using a protractor.

Talar head and neck

The breadth of the talar head (THB) was taken in a mediolateral plane, to achieve a maximum breadth, and the talar head depth (THD) was taken as the maximum distance between the inferior and superior aspects. The talar head and neck length (THNL) was derived by measuring the length of the talus (TL) from the most ventral point of the talar head to the dorsal point of the trochlea, in line with the direction of the talar head and neck, and subtracting the length of the talar trochlea (TTL). Similarly to the method used for ascertaining the angle for the curvature of the posterior calcaneal facet, the angle of direction of the talar head (ATH-LC) was derived by placing the talus on the trochlea, with the lateral crest in a horizontal plane, and drawing the direction of projection of the head and neck. The angle was then measured from the diagrams using a protractor. This measurement was slightly different to the measure used by Langdon (1986) from which the fossil data derives. Langdon, however, used lines of measurement that approximate the perpendicular to the lines used here (long axis of the talonavicular facet and the line of the trochlea breadth are perpendicular to the talar head and neck projection and lateral crest, respectively), and therefore the resulting angle is the same and can be meaningfully compared between the fossil and extant genera.

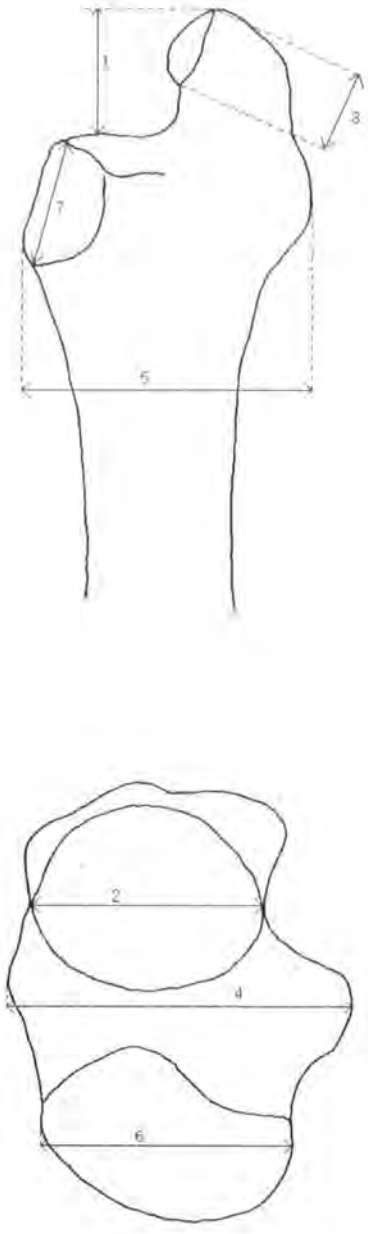

Figure 1:Ulna measurements top to bottom, distal ulna lateral and distal views (1. ulna styloid process length, 2. carpal articular facet mediolateral breadth, 3. carpal articular facet anteroposterior breadth, 4. ulna head mediolateral breadth, 5. ulna head anteroposterior breadth, 6. radial facet mediolateral breadth, 7. radial facet proximodistal height)

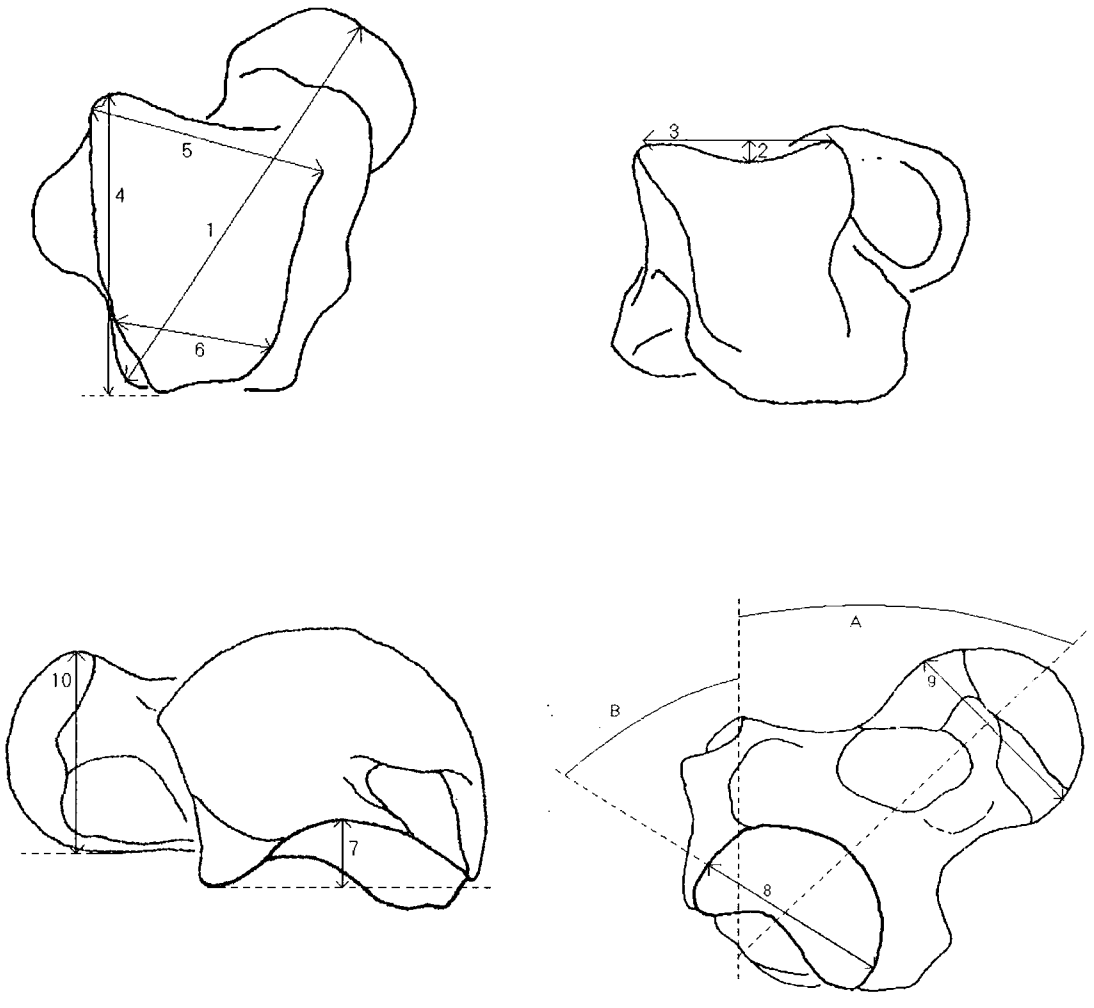

Figure 2: Talus measurements (after Strasser, 1988) clockwise from top left, proximal, dorsal, plantar and lateral views, (1. talus length, 2. talar trochlea depth, 3. breadth of the talar trochlea between the most superior points of the medial and lateral crests, 4. talar trochlear length, 5. talar trochlear anterior breadth, 6. talar trochlea posterior breadth, 7. posterior calcaneal facet depth, 8. posterior calcaneal facet length, 9. talar head breadth, 10. talar head depth, A. angle of curvature of posterior calcaneal facet to the lateral crest, B. angle of projection of talar head and neck from lateral crest)

DERIVED MEASUREMENTS

Wrist indices

The wrist indices used in this study were devised primarily as a measurement of ulna deviation from the carpus, which has been proposed as a derived hominoid characteristic pertaining to locomotor differences from the ancestral catarrhine.

Measurement	Description	Calculation
Ulna		
Ulnocarpal joint		
IUSPL	Index of ulna styloid process length	100. (USPL / UMSA)
IUSPL2	Index of ulna styloid process length 2	100. (USPL / UHA)
IUCA	Index of ulnocarpal articulation	100. (UCFA / UMSA)
Radioulnar joint		
IUHS	Index of ulna head shape	100. (UH-ML / UH-AP)
IRUA	Index of radioulnar articulation	100. (URF-ML / UH-AP)
IRUAFS	Index of radioulnar articular facet shape	URF-ML / URF-PD
Talus		
Talocrural joint		
ITD	Index of talar trochlea depth	100. (TTD / TTB)
IAPTW1	Index of anteroposterior trochlea wedging 1	100. (TTAB / TTPB)
IAPTW2	Index of anteroposterior trochlea wedging 2	100. (TTAB – TTPB) / TTL
Subtalar joint		
IPCFD	Index of posterior calcaneal facet depth of curvature	100. (TPCFD / TPCFL)
ASTA-LC	Angle of subtalar axis to lateral crest	90°- ACPCF-LC
Talar head and neck		
ITHB1	Index of talar head breadth 1	100. (THB / TTB)
ITHB2	Index of talar head breadth 2	100. (THB / THD)
ITHNL	Index of talar head and neck length	100. THNL / TTL)
ATH-LC	Angle of talar head projection to lateral crest	

Table 7: Derived measurements

Ulnocarpal joint

IUSPL. 100. (USPL / UMSA)

This first index describes the withdrawal of the ulna styloid process from articulation with the carpus, and a lower index would be indicative of a relatively shorter ulna styloid process, and thus less contact with the carpus. This study initially used a mid-shaft cross-sectional area measurement to calculate the indices and eliminate body size variables, rather than a single ulna head diameter measurement as used in other studies (Larson, 1998). This was due to the variation in ulna head shape found among primates (most particularly the hominoid distal ulna differs in shape from that of cercopithecoids in being anteroposteriorly short and broad). The current measurement was therefore devised to eliminate any confounding variables.

IUSPL2. 100. (USPL / UMSA)

This second index of ulna styloid process length was devised primarily to offer a comparison between the fossil and extant genera, due to the lack of mid-shaft and distal ulna data from individual specimens. Again, in order to eliminate distortion of results that might be caused by variability in head shape, a cross-sectional area measurement was used rather than a single breadth measurement.

IUCA. 100. (UCFA / UHA)

This index quantifies the area of the articular facet on the ulna styloid process for the triquetral and pisiform, to gauge the extent of ulnocarpal articulation. A lower value would be indicative of reduced articulation between the ulna and the carpus. This may be complicated by the presence of an intra-articular meniscus in hominoids, and the difficulties associated with distinguishing articulation with the carpus from that with the meniscus.

Radioulnar joint

IUHS. 100. (UH-ML / UH-AP)

This index provides an estimate of ulna head shape, and is derived from the mediolateral and anteroposterior diameters of the ulna head. Higher values suggest an ulna head that is mediolaterally broad, and anteroposteriorly shallow.

IRUA. 100. (URF-ML / UH-AP)

This is an index of the extent of the radial facet on the ulna head relative to the anteroposterior breadth of the ulna head. This reflects of the amount of rotation of the ulna head in relation to the radius, and thus the degree of ulna deviation facilitating pronation-supination. Higher values would be expected where ulna deviation is more significant.

IRUAFS. URF-ML / URF-PD

This index is describes the shape of the radial facet on the ulna head, and is derived from the mediolateral length and the maximum transverse breadth (orientated proximodistally, anteroposteriorly, or obliquely between these extremes) of the articular surface.

Ankle indices

The trochlear indices pertain to the talocrural joint, and those of the posterior calcaneal facet to the subtalar joint. The head shape and orientation, and the head and neck length are relevant for both the subtalar and midtarsal joints. The primary motion at the talocrural joint is plantarflexion/dorsiflexion, with medio-lateral rotation. In the subtalar joint, however, motion is predominantly inversion/ eversion. This latter is of particular interest for cautious quadrupedal climbing, in the foot's accommodation to inclined surfaces. The other ranges of motion are also important for the general mobility at the ankle, essential for grasping quadrupedal/climbing postures.

Talocrural joint

ITD. 100. (TTD / TTB)

This index of trochlear depth is derived from the depth of the talar trochlear trough relative to trochlear breadth. The relative depth is significant as it pertains to the congruency of the joint, and thus the range of accessory motion possible at the talocrural joint. A shallow relative depth indicates a less closely packed joint and thus a greater degree of mobility.

IAPTW1. 100. (TTAB / TTPB)

Both this index, and the next, quantify the shape of the talar trochlea, from a superior aspect, and are measurements of the anteroposterior 'wedging' of the trochlea. Wedging occurs when the lateral and medial trochlear crests diverge from one another towards their anterior margins, and converge at their posterior limits. Trochlear wedging allows different degrees of accessory movement at the talocrural joint in dorsiflexed and plantarflexed positions, with the latter having a greater degree of mediolateral mobility, and the former being more closely packed. This first index is a ratio of the anterior and posterior breadths, and a higher value represents a larger difference between these measurements and thus increased wedging.

IAPTW2. 100. (TTAB – TTPB)/TTL

This second index of trochlear wedging is again a measure of the difference between the anterior and posterior breadths of the trochlea, but also incorporates the anteroposterior length of the trochlea to give a better indication of the degree of wedging in relation to the overall trochlea size. Once more, a higher value denotes greater range of mobility in plantarflexed postures.

Subtalar joint

IPCFD. 100. (TPCFD / TPCFL)

This index is a gauge of the relative depth of the posterior calcaneal facet in relation to the maximum length of the facet along the axis of curvature. A deeply curved trochlear would indicate greater rigidity of the subtalar joint, as the opposite calcaneal articular surface is more tightly wrapped. Conversely, extra mobility is offered by the less congruent joint indicated by a relatively shallower facet.

ASTA-LC 90°- ACPCF-LC

The direction of curvature of the posterior calcaneal facet is perpendicular to the axis of movement at this point (subtalar axis), and thus the angle of the subtalar axis from the lateral crest was calculated by subtracting the original angle from 90. The angle of this axis from the lateral crest (where the anteroposterior orientation of the lateral crest is taken to denote the longitudinal axis of the foot) is related to the amount of mediolateral rotation and plantar/dorsiflexion that takes place at the subtalar joint during the joint's primary movement of inversion/eversion. If the subtalar axis were parallel to the longitudinal axis (i.e., angle = 0°), then the main movement possible would be inversion/eversion, whilst with a perpendicular axis (i.e., angle = 90°) the primary movement becomes plantar/dorsiflexion. Both of these scenarios would allow little accessory movement. In general, however, primates exhibit neither of these extremes. With greater obliquity of the subtalar axis from the longitudinal axis, the foot attains mediolateral mobility, becoming laterally rotated in inversion, and medially rotated in eversion. As the axis approximates the perpendicular, however, inversion/eversion and mediolateral rotation become limited, as the primary motion is brought into the longitudinal plane.

Talar head and neck

ITHB1. 100. (THB / TTB)

Both this and the next index are measures of talar head breadth. The first index quantifies the talar head breadth in comparison to the talar trochlear breadth, and thus gives an indication of the robusticity of the head in relation to other structures of the talus, and the extent of the talonavicular articulation. Hence the relative size of this aspect of the talus is important for discerning the degree of mobility at the talonavicular joint. A high value suggests a mediolaterally broad head relative to the mediolateral breadth of the trochlea.

ITHB2. 100. (THB / THD)

This second breadth index is a ratio of talar head breadth to talar head depth, and thus gives an indication of the overall talar head shape from an anterior view. As a result, higher values suggest a broad head relative to its craniocaudal height. Again, this is important for the talonavicular articulation, in that a broader head suggests greater excursion at this point.

ITHNL. 100. (THNL / TTL)

The index of talar head and neck length is derived from the talar head and neck length and the overall trochlea length, and provides information as to the relative proportions of the talus. A relatively short neck and head suggests greater robusticity.

ATH-LC.

The angle of talar head and neck projection is related to the direction of forces incurred during locomotion. A medially orientated head and neck, relative to the longitudinal axis of the foot (represented here by the lateral crest) means that stresses during activity are orientated medially, which might be related to the grasping function of the hallux, and the weight bearing function of the medial side of the foot. If the talar head and neck are orientated more into the longitudinal axis

of foot, the major stresses at this point will be focused towards the direction of forward motion.

STATISTICAL ANALYSIS

Calculations, analyses of results and graphs were all derived using SPSS for Windows 9.0. The results for each index were illustrated by box and whisker plots. A solid black line within the 'box' illustrates the mean values for each taxon and the extremes of the 'whiskers' illustrate the range of values observed (with the exception of extreme outliers, which are represented by numbered symbols). One-way ANOVA multiple comparison tests were also conducted, at the family level, although the great apes were futher divided into African apes and *Pongo* due to the huge differences between these taxa. For the test of homogeneity of variance all of the indices and angles were significant at $p< 0.05$, so the non-parametric Games-Howell multiple comparison test for heterogeneous subsets was applied. These results are illustrated in tables to show the primate divisions that did not differ significantly from one another for each variable.

CHAPTER 6

Results

ULNOCARPAL JOINT

Lorisidae

The ulna styloid process in *Nycticebus* is long and more or less hook-like. A smooth, convex articular surface is present on the tip of the ulna styloid process for articulation with the carpus, the bulk of which faces the interior of the joint. In *Arctocebus*, the ulna styloid process is again hook-like, but flattened distally. The articular facet for the carpus is situated on the medial/interior sides of the flattened tip. The *Loris* ulna styloid process is mediolaterally thin and hook-like, and flattened on its distal aspect. The facet for the carpus is situated on this flattened tip and is orientated medially or more towards the interior of the joint. The ulna styloid process in *Perodicticus* is very long, and more or less hook-like. The carpal facet on the ulna styloid process is small and orientated anterodistally.

Despite variation both between and within genera, all of the lorises possess a long, thin hook-like ulna styloid process, to a greater or lesser degree, with flattened or convex articular surfaces orientated predominantly towards the interior of the ulnocarpal joint.

Lemuridae

The ulna styloid process in *Varecia* is quite short and stubby, with a large, almost 'ball-like' carpal facet covering all distal and peripheral aspects of the tip, although limited towards the dorsal side.

Cebidae

Saimiri ulna styloid processes are small and robust, articular for the carpus on its distal and interior aspects. In some specimens, the carpal facet covers the whole of

the distal aspect of the ulna styloid process, verging to the medial and lateral sides, the interior, and slightly onto the posterior surface.

Atelidae

The ulna styloid process of *Chiropotes* is variable, with some slightly hook-like, and some not. The styloid is articular on its distal extremity. The carpal facet in some specimens extends to the medial and lateral sides of the ulna styloid process, less so ventrally and not markedly dorsally. In *Alouatta*, the carpal facet on the ulna styloid process covers the whole of the distal aspect, extending to the interior, medial and lateral sides, and in some specimens, articular on the outside of the joint. The ulna styloid process is quite short and stubby.

Cercopithecidae

The ulna styloid process of *Cercopithecus* is often not very long, but in some specimens very hooked, curving over the radial facet. It is articular predominantly on its interior and distal aspects, extending medially and laterally in some specimens. The *Macaca* ulna styloid process is long, and hook-like (to varying degrees). The large carpal facet is situated on its distal end, extending round all aspects as a conical articulation, and is especially prominent on the dorsal slope of the ulna styloid process. The specimens showed very clear articulations for both the carpus and the radius.

Hylobatidae

Hylobates has a fairly long, thin and hook-like ulna styloid process, leaning well over the radial facet, with an articular facet for the carpus on the convex distal aspect that extends over to the dorsal aspect of the ulna styloid process. In some specimens, a more or less distinguishable point was found on the tip of the articular facet, perhaps indicating a different type of articular contact.

Great apes

The ulna styloid process in *Gorilla* is markedly reduced, almost the same size as the radial facet portion of the head, and although hook-like in some specimens, it

is very short. The ulna styloid process is sometimes large and flat on its distal extremity, and other times tapers more to a smaller flattened end, but is always convex to greater or lesser degree.

In some *Pan* specimens, the ulna styloid process is quite hook-like, although others are rather long and straight, perhaps bulging dorsally, but with no evidence of a hook. It is quite difficult to distinguish the articular facet on the end of the ulna styloid process in some specimens, but a flattened surface, which seems articular (possibly with a meniscus), is generally apparent in these specimens. There is no obvious evidence of a distinct facet for the triquetral in most of the specimens, although some specimens have a slight point on the end. One particular specimen appeared to have two well-defined facets, one within the other, which may reflect the tip articulating with the triquetral, and the periphery with the meniscus. Another specimen appears to possess two connected facets, the second situated to the rear of the first, trailing down the back of the ulna styloid process. The shape and orientation of the facet varied, depending upon the shape of the ulna styloid process. Generally, however, the carpal facet is directed distomedially or distodorsally, sometimes taking the form of a conical tip, but often on the flattened distal extremity of the process.

The *Pongo* ulna styloid process is highly varied, sometimes short, and very straight, and in other specimens very long and slightly hook-like. In one specimen the short ulna styloid process shows a considerable dorsal 'lean' away from the ulna head. The articular surface for the carpus is generally orientated distally and towards the interior of the joint, although one is more dorsally placed. The shape of the facet varies too; sometimes short and flat, and in other cases taking the form of a conical articular tip.

The great ape ulna styloid processes show huge variation, both within and between genera, in terms of all aspects of the size, shape and orientation of both the ulna styloid process itself and its articular facets. It is hence quite difficult to summarise a 'typical' morphology purely on the basis of these observations.

IUSPL

Pan, *Pongo* and *Gorilla* all display very low means for this first index of ulna styloid process length, indicating a much reduced ulna styloid process, and very small ranges of variation (Table 8). These results are considerably lower than any other taxa studied. The lorises, on the other hand exhibit very high index of ulna styloid process length, at the other extreme within the range of primates considered, suggesting the ulna styloid process to be comparatively long. *Arctocebus* has by far the longest ulna styloid process, with a mean of 69.714. Interestingly, *Hylobates* is more similar to *Alouatta* and the cercopithecoids than to the other hominoids.

Genus	Number	Mean	Range
Gorilla	22	0.555	0.215 - 1.094
Pongo	20	1.128	0.224 - 1.807
Pan	20	2.354	1.311 - 4.075
Hylobates	20	9.426	5.404 - 11.797
Alouatta	17	9.474	6.235 - 16.720
Macaca	20	10.210	6.488 - 16.779
Cercopithecus	20	11.699	6.807 - 17.235
Chiropotes	5	13.377	10.969 - 18.111
Varecia	9	15.855	7.016 - 23.492
Saimiri	22	19.775	13.294 - 26.756
Nycticebus	14	35.505	23.700 - 53.748
Perodicticus	21	36.945	23.263 - 70.525
Loris	5	56.363	42.869 - 76.441
Arctocebus	3	69.714	53.981 - 77.791

Table 8: IUSPL means and ranges

The plot clearly shows the relationships between the taxa; lorises exhibit a distinctly different morphology from the other primates, with much larger ranges of variation (Figure 3). The diagram also shows that the great apes are quite different from the other taxa, with a consistently very low index of ulna styloid process length, and limited variability.

The multiple comparisons test highlights the above observations most clearly (Figure 5). The great apes (African apes and *Pongo*) and Lorisidae, at opposite extremes of the primate range, both exhibit unique morphologies, with their means differing from all the other families at the 95% confidence level. The

Hylobatidae, although converging towards the great ape character state, are closely aligned with the atelines and cercopithecoids in this character, showing no significant mean difference from these two groups.

IUSPL2

This second index of ulna styloid process length shows very much the same sort of pattern as the previous index, with only minor variations in the mean values of some of the monkey and lorisid taxa (Table 9). In this analysis, however, it was possible to incorporate proconsulids, and both *Kalepithecus* and *Proconsul* showed values between those of *Hylobates* and the monkeys. This is further illustrated on the plot for this index (Figure 4).

Genus	Number	Mean	Range
Gorilla	22	0.313	0.110 – 0.610
Pongo	20	0.574	0.110 – 1.020
Pan	20	1.183	0.690 – 1.950
Hylobates	20	5.170	2.420 – 8.580
**Kalepithecus*	1	5.310	-
**Proconsul*	1	6.210	-
Macaca	20	6.336	4.500 – 8.900
Alouatta	17	6.612	4.610 – 11.650
Cercopithecus	20	7.835	4.570 – 10.430
Varecia	9	10.913	8.720 – 13.240
Chiropotes	5	12.937	11.130 – 14.840
Saimiri	22	14.879	11.320 – 21.640
Nycticebus	14	22.494	15.380 – 31.340
Perodicticus	21	22.691	13.500 – 34.620
Arctocebus	3	30.087	24.720 – 36.510
Loris	5	43.491	31.330 – 68.900

Table 9: IUSPL2 means and ranges (fossils indicated by *)

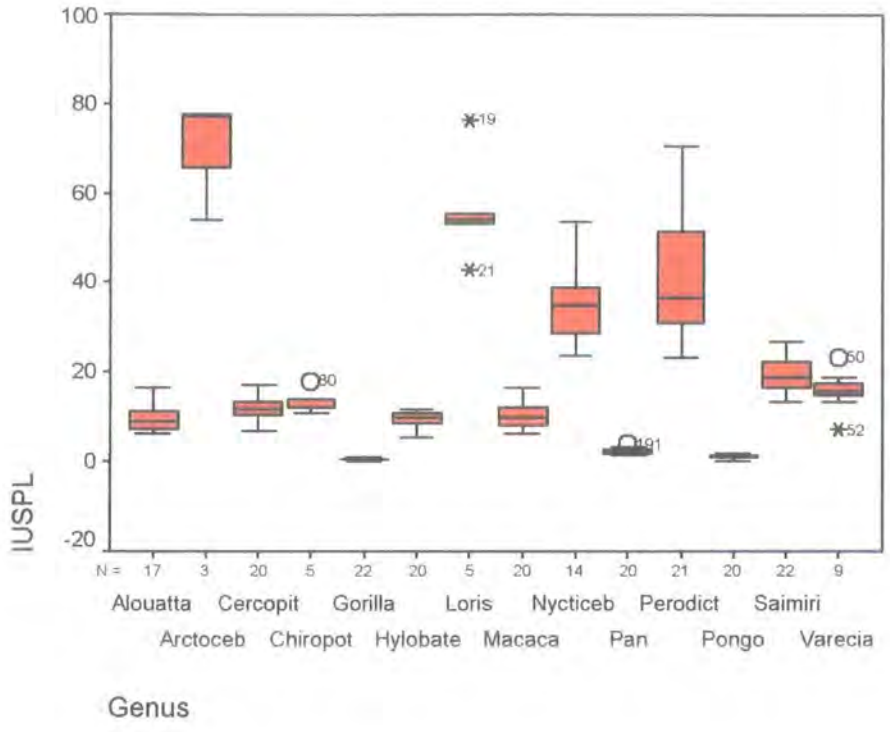

Figure 3: IUSPL boxplot showing means and ranges by genus

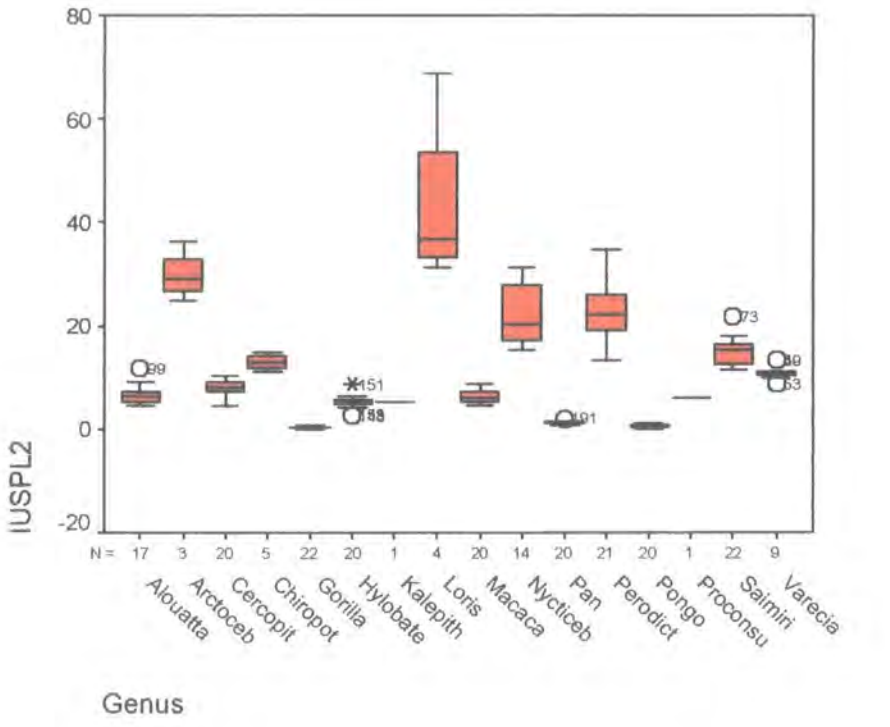

Figure 4: IUSPL2 boxplot showing means and ranges by genus

Taxonomic grouping	*Pongo*	African apes	Hylobatidae	Atelidae	Cercopithecidae	Lemuridae	Cebidae	Lorisidae
Pongo	x	x						
African apes	x	x						
Hylobatidae			x	x	x			
Atelidae			x	x	x	x		
Cercopithecidae			x	x	x	x		
Lemuridae				x	x	x	x	
Cebidae						x	x	
Lorisidae								x

Figure 5: IUSPL multiple comparison between taxonomic groups (x denotes no significant mean difference, p<0.05)

Taxonomic grouping	*Pongo*	African apes	Hylobatidae	Proconsulidae	Cercopithecidae	Atelidae	Lemuridae	Cebidae	Lorisidae
Pongo	x	x		x					
African apes	x	x		x					
Hylobatidae			x	x					
Proconsulidae	x	x	x	x	X	x			
Cercopithecidae				x	X	x			
Atelidae				x	X	x			
Lemuridae							x		
Cebidae								x	
Lorisidae									x

Figure 6: IUSPL2 multiple comparison between taxonomic groups (x denotes no significant mean difference, p<0.05)

The multiple comparison test for this second index of ulna styloid process length demonstrates the intermediate nature of this characteristic in the proconsulids, between *Hylobates* and the cercopithecoids but, due to the few numbers of fossil specimens, this cannot necessarily be taken as an accurate representation, and the analysis also suggests no mean difference (at $p<0.05$) from the results obtained for the great apes.

IUCA

For the index of ulnocarpal articulation the great apes show significantly lower values than all other taxa, indicating a reduction in direct ulnocarpal contact in these genera (Table 10). *Nycticebus* and *Perodicticus* have the next lowest mean values. The ulnocarpal index of *Hylobates* is most similar to those of *Alouatta*, *Chiropotes*, *Cercopithecus*, *Macaca*, and *Loris;* means for all of these genera fall between 33 and 42. It is interesting to note that three of the four lorisids genera fall within the range of means exhibited by the hominoids. Again, the mean value for *Arctocebus*, and to a lesser extent that of *Loris*, is slightly higher than that of the other lorisids. The genera exhibiting the highest ulnocarpal articulation are *Varecia* and *Saimiri*.

Genus	Number	Mean	Range
Pongo	20	11.998	8.100 - 18.898
Gorilla	22	14.926	5.474 - 29.754
Pan	20	16.444	8.681 - 29.485
Perodicticus	19	23.506	9.628 - 89.506
Nycticebus	11	23.715	9.678 - 33.364
Loris	3	33.419	22.823 - 41.578
Hylobates	20	35.060	21.154 - 53.659
Chiropotes	5	35.704	25.379 - 51.735
Cercopithecus	20	40.127	21.551 - 69.332
Alouatta	17	41.556	23.382 - 60.694
Macaca	20	42.328	30.842 - 79.389
Arctocebus	2	42.963	37.067 - 48.859
Saimiri	22	48.610	27.399 - 83.475
Varecia	9	77.148	31.184 - 94.403

Table 10: IUCA means and ranges

The plot (Figure 7) suggests again that the great apes are a cohesive group in this index, with uniformly low mean ulnocarpal values. *Hylobates*, however, exhibits ulnocarpal articulation apparently more consistent with New and Old World monkeys and some of the lorisids. It is quite difficult to determine the relationship of the lorises from this diagram, as the different genera vary in their means and ranges.

The multiple comparisons test for this index gives a better indication for the position of the lorises within the primate range, finding them to be intermediate between the great apes and hylobatids in this character, with no significant difference between the Lorisidae and Hylobatidae means at the 95% confidence level (Figure 9). The great ape ulnocarpal articulation is significantly different to all of the other groups at this level, with *Pongo* exhibiting the most extreme articular facet reduction. Hylobatids also show similarities to both cercopithecids and atelids.

RADIOULNAR JOINT

Lorisidae

The radial facet in *Nycticebus* is large, and situated on the distal aspect of the ulna head, and although it does not extend round the ulna head and is more square in shape. It is, however, still fairly extensive. In *Arctocebus*, the articular surface for the radius is distally orientated and extends around the ulna head. In *Loris*, the articular surface on the ulna head for the radius extends round the head. The very large radial facet of *Perodicticus* is orientated distally on the ulna head, but is square rather than extending round the head.

Lemuridae

The *Varecia* radial articulation is very small, and borne on a short projection on the head, facing the interior of the joint.

Cebidae

The radial facet in *Saimiri* is limited in its extent, projecting slightly from the head and orientated both distally and towards the interior of the joint. In some specimens the radial facet is virtually indiscernible.

Atelidae

The ulna head in *Chiropotes* shows limited radial articulation and in *Alouatta* the radial facet is very small, on a small stubby projection, and is almost indistinguishable from the rest of the head.

Cercopithecidae

In *Cercopithecus*, the radial facet, borne on a small stub-like projection, faces distally. Although the radial facet is small, it extends medially and laterally, but not to the same extent as in hominoids. The radial articulation on the ulna head in *Macaca* is separated from the ulna styloid process by quite a wide groove. The radial facet is orientated towards the interior of the joint, but extends round slightly medially and laterally in some specimens, and is small and square in others.

Hylobatidae

In *Hylobates*, the radial facet is longer mediolaterally than in the cercopithecids, but not to the same extent as seen in the great apes, and orientated towards the interior of the joint, and on the distal aspect. The radial articulation was separated from the ulna styloid process by a shallow but fairly wide groove.

Great apes

In *Gorilla*, a huge groove is evident between the radial facet-bearing portion of the head and the ulna styloid process. The former projects, forming a large curved extremity around the ulna styloid process. The radial facet is very large, extending around the head on its distal and anterior aspects. In *Pan*, the radial facet curves around the extent of the ulna head, in a similar way to that of *Gorilla*. The

enormous *Pongo* radial facet extends all the way around the head and contacts the base of the ulna styloid process on the medial side. The radial facet is orientated towards the distal aspect in some specimens, and towards the interior of the joint in others.

The radial facet in the great apes is comparatively large and extends around the ulna head to form a long, smooth and relatively thin convex band for articulation with a mobile radius.

IUHS

For the index of ulna head shape (Table 11) the hominoid genera on the whole show the highest means, with the great apes (and especially *Pongo*) exhibiting the greatest extreme. An ulna head shape index approximating 100 would suggest an ulna head that has equal mediolateral and anteroposterior breadths, whilst a mediolaterally narrow ulna head would be represented by a much lower index. Although all of the great apes have high indices, with ranges exceeding 100, the means all fall below this value. *Gorilla*, however, has a huge range of variation for this index, with a highest value of almost 140. *Varecia* also exhibits a relatively high index, exceeding that of *Hylobates*. These genera are closely followed by the loris taxa. The hominoids, on the whole, show more similarity to the strepsirhines than to any other primates.
It was possible to look at two fossil specimens for this index. *Kalepithecus* has a low index of ulna head shape, falling well within the range shown for the monkey taxa, whilst *Proconsul* is more similar to the lorisids.

The plot (Figure 8) for this index illustrates well the different ulna head shape seen in the great apes, and to a lesser extent V*arecia*, with *Hylobates* and the lorisids exhibiting a more moderate form of this morphology, essentially intermediate between monkeys and the great apes. The remaining taxa are all fairly similar to one another, clustering between 70 and 80 in this feature. The fossil specimens are evidently most similar to the monkey genera in this feature.

Genus	Number	Mean	Range
Macaca	20	72.780	61.803 - 83.784
Alouatta	17	72.788	63.296 - 83.529
**Kalepithecus*	1	73.080	-
Saimiri	22	73.297	58.597 - 88.209
Cercopithecus	20	74.864	65.948 - 86.902
Chiropotes	5	74.937	60.955 - 85.841
Perodicticus	21	75.337	62.069 - 90.642
Loris	4	76.477	70.805 - 84.615
**Proconsul*	1	78.330	-
Nycticebus	14	79.532	63.594 - 94.715
Arctocebus	3	81.646	77.186 - 85.276
Hylobates	20	82.015	72.593 - 93.168
Varecia	9	88.073	77.290 - 108.511
Pan	20	91.549	78.448 - 104.723
Gorilla	22	94.302	80.000 - 139.771
Pongo	20	96.377	84.971 - 105.511

Table 11: IUHS means and ranges (fossils indicated by *)

The multiple comparison test finds no significant mean difference between the great apes and *Varecia* at the 95% confidence level, and *Varecia* is also not significantly different to the hylobatids and lorisids (Figure 10). The monkey genera, at the opposite extreme from the hominoids, also show no significant difference from the lorisids, which reiterates the intermediate nature of the loris morphology. The fossil ulnae show no significant mean differences to any other taxa, probably due to the limited numbers of specimens available, but the structure of these specimens indicates a morphology somewhere between that seen in lorises and cercopithecoids.

IRUA

For the index of radioulnar articulation the hominoids show a much larger mean value than other genera, most closely matched by *Loris* and *Arctocebus*, and to a lesser extent *Nycticebus* (Table 12). *Pongo* exhibits the most extreme mean value overall. This high value is indicative of a relatively extended radial articulation on the ulna, and thus increase potential excursion of the radius around the ulnar head.

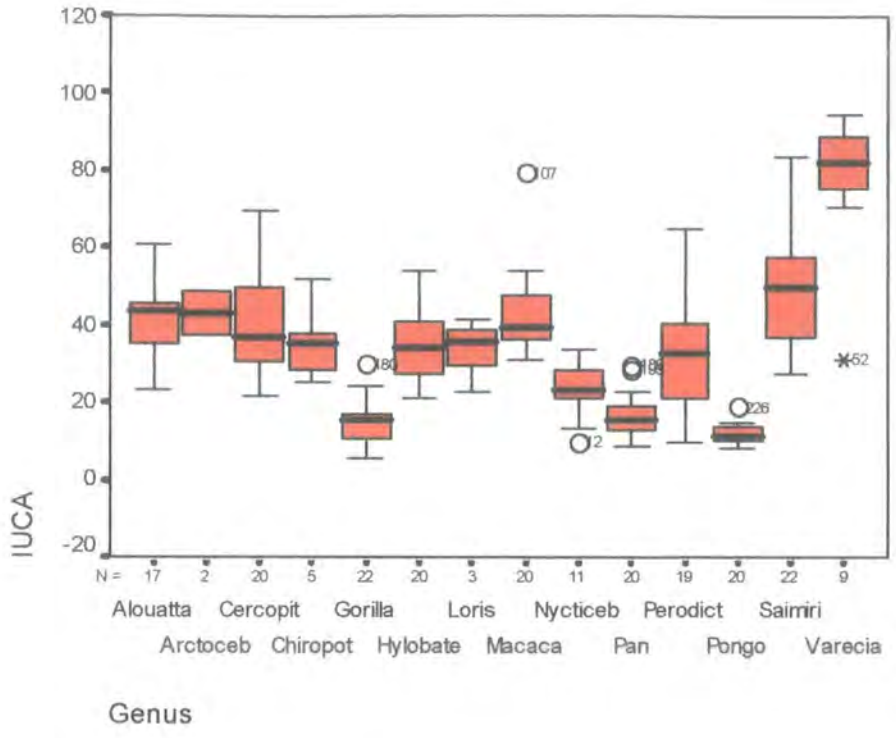

Figure 7: IUCA boxplot showing means and ranges by genus

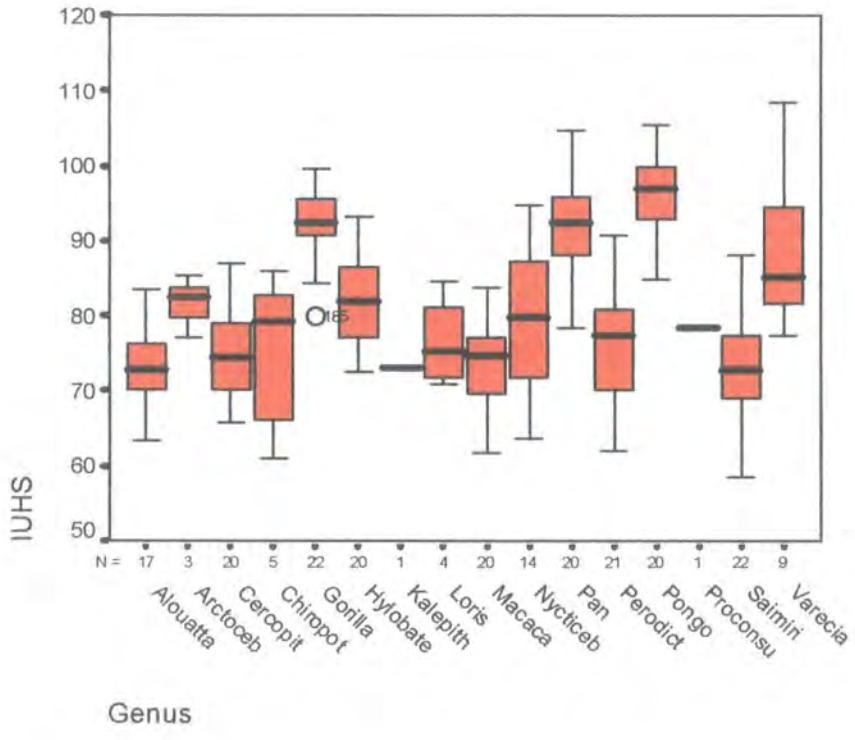

Figure 8: IUHS boxplot showing means and ranges by genus

Taxonomic grouping	*Pongo*	African apes	Lorisidae	Hylobatidae	Atelidae	Cercopithecidae	Cebidae	Lemuridae
Pongo	x							
African apes		x						
Lorisidae			x	x				
Hylobatidae			x	x	x	x		
Atelidae				x	x	x	x	
Cercopithecidae				x	x	x	x	
Cebidae					x	x	x	
Lemuridae								x

Figure 9: IUCA multiple comparison between taxonomic groups (x denotes no significant mean difference, p<0.05)

Taxonomic grouping	Atelidae	Cebidae	Cercopithecidae	Proconsulidae	Lorisidae	Hylobatidae	Lemuridae	African apes	*Pongo*
Atelidae	x	x	x	x	x				
Cebidae	x	x	x	x	x				
Cercopithecidae	x	x	x	x	x				
Proconsulidae	x	x	x	x	x	x	x	x	x
Lorisidae	x	x	x	x	x	x			
Hylobatidae				x	x	x	x		
Lemuridae				x	x	x	x	x	x
African apes				x			x	x	x
Pongo				x			x	x	x

Figure 10: IUHS multiple comparison between taxonomic groups (x denotes no significant mean difference, p<0.05)

The New World genera and *Varecia* show the lowest values for this index, indicative of a relatively restricted radioulnar articulation, whilst the cercopithecids exhibit values that are somewhat intermediate in the primate range and comparable to *Perodicticus*.

Genus	Number	Mean	Range
Chiropotes	5	34.560	29.830 – 39.580
Varecia	9	41.309	30.720 – 54.550
Saimiri	21	42.315	26.700 – 55.000
Alouatta	17	46.794	36.170 – 62.820
Cercopithecus	20	55.260	40.490 – 71.970
Perodicticus	21	57.149	36.950 – 69.960
Macaca	20	59.016	46.260 70.040
Nycticebus	14	63.354	48.300 – 86.680
Arctocebus	3	67.268	64.610 – 71.860
Loris	4	72.944	67.450 - 78.630
Hylobates	20	80.867	72.100 - 90.220
Gorilla	22	89.150	78.970 – 96.650
Pan	20	89.635	78.390 – 95.890
Pongo	20	94.212	78.520 – 114.840

Table 12: IRUA means and ranges

These results are illustrated on the plot, which clearly shows the high values found in the ape genera, and the apparent convergent morphology seen in some of the lorisids (Figure 11). The lemurids, cebids and atelids are visibly at the opposite extreme to the hominoids in this index, and the cercopithecids somewhat in-between. The multiple comparison test reveals no significant mean difference within the great apes, but the hylobatids are found to be different to all other taxa, despite having a morphology between that of the other apes and the lorisids (Figure 13). The lorisids are somewhat intermediate between the extreme groupings, showing no mean difference to the cercopithecids at the 95% confidence level. The New World families and *Varecia* are clearly very similar in this aspect of their morphology, exhibiting no significant mean difference at 95% confidence. These taxa are at the opposite extreme of the primate range to the hominoids.

IRUAFS

For index of radioulnar articular facet shape, the hominoids all show uniformly high means in comparison to the other taxa, indicating a mediolaterally long radioulnar articular facet in these genera, and thus greater potential excursion of the radius around the ulna (Table 13). The closest genera to the apes are *Loris*, *Arctocebus* and *Nycticebus*, but *Perodicticus* is more similar in its range and mean to *Alouatta*, *Cercopithecus*, *Macaca* and *Saimiri*. The lowest values are seen in *Varecia* and *Chiropotes*, which, with values of <100, suggest an articular surface longer anteroposteriorly than mediolaterally.

Genus	Number	Mean	Range
Varecia	9	81.631	59.045 - 94.022
Chiropotes	5	94.142	72.376 - 120.231
Saimiri	21	128.127	72.170 - 200.000
Perodicticus	21	139.917	79.026 - 183.333
Cercopithecus	20	146.587	102.381 - 207.985
Alouatta	17	157.086	97.313 - 240.164
Macaca	20	167.130	94.216 - 268.718
Nycticebus	14	171.206	101.914 - 250.413
Arctocebus	3	193.523	181.731 - 200.943
Loris	4	195.602	141.429 - 266.667
Gorilla	22	217.539	179.563 - 266.162
Hylobates	20	219.601	139.035 - 307.850
Pongo	20	237.916	166.607 - 337.423
Pan	20	247.348	196.429 - 307.715

Table 13: IRUAFS means and ranges

The plot highlights the uniformly high index of radioulnar articular facet shape in the hominoids, and shows the close affinities of some of the loris genera to this character state in their means and ranges (Figure 12). As the diagram is somewhat clustered for many of the other taxa, and the ranges are fairly varied, it is quite difficult to elucidate any definite relationships among the remaining taxa.

The multiple comparison test for the shape of the radioulnar articulation (Figure 14) shows the lorises to occupy an intermediate position between the hominoids and the other genera, remaining more similar to the hylobatids and great apes than any other taxa, although the former are different to all the hominoid divisions at the 95% significance level.

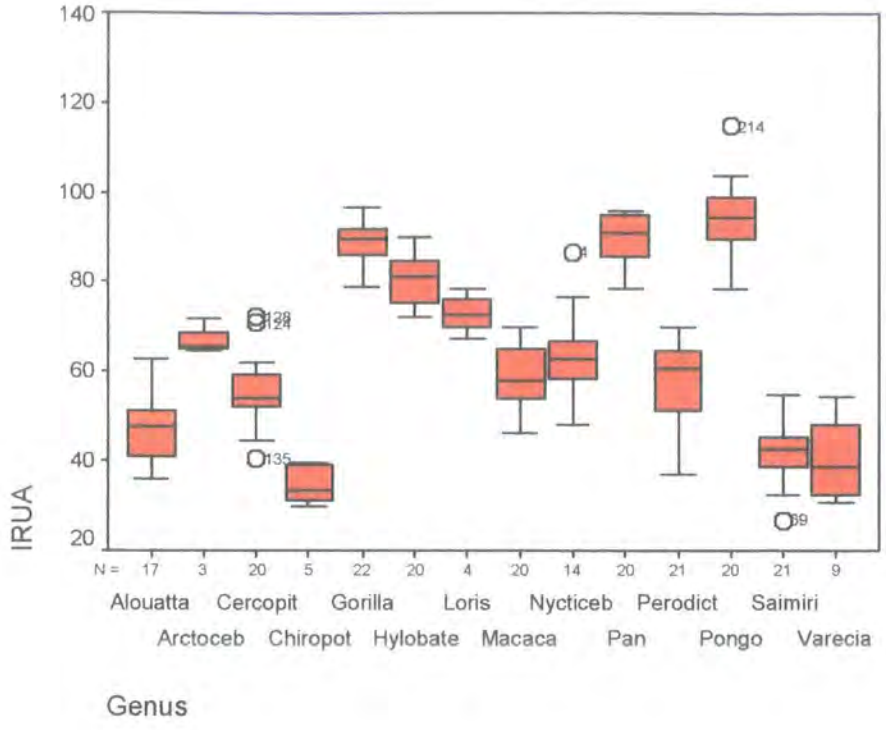

Figure 11: IRUA boxplot showing means and ranges by genus

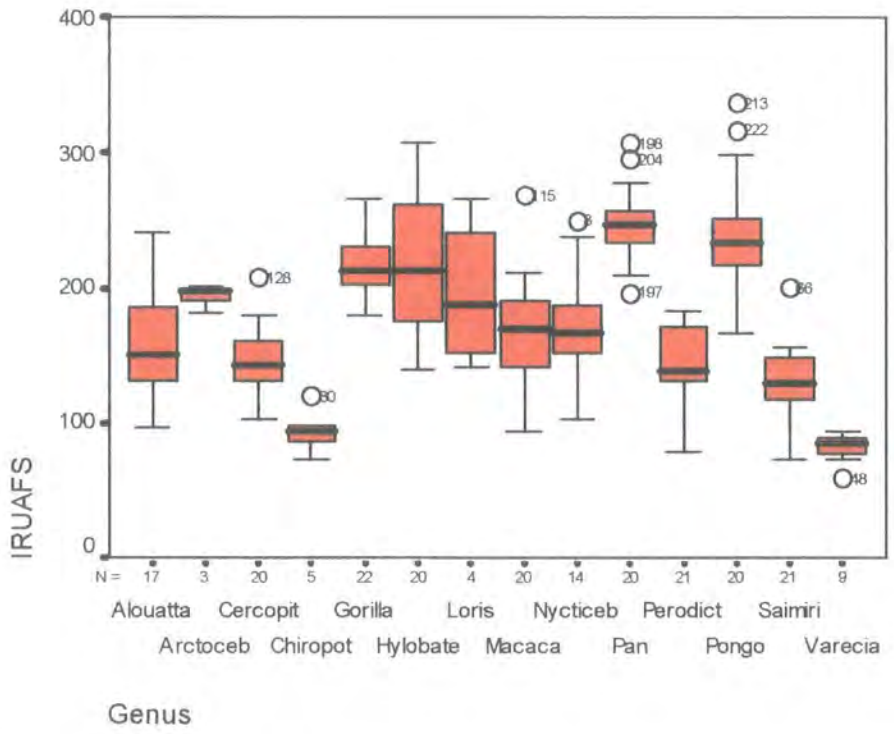

Figure 12: IRUAFS boxplot showing means and ranges by genus

Taxonomic grouping	Lemuridae	Cebidae	Atelidae	Cercopithecidae	Lorisidae	Hylobatidae	African apes	*Pongo*
Lemuridae	x	x	x					
Cebidae	x	x	x					
Atelidae	x	x	x					
Cercopithecidae				x	x			
Lorisidae				x	x			
Hylobatidae						x		
African apes							x	x
Pongo							x	x

Figure 13: IRUA multiple comparison between taxonomic groups (x denotes no significant mean difference, p<0.05)

Taxonomic grouping	Lemuridae	Cebidae	Atelidae	Cercopithecidae	Lorisidae	Hylobatidae	African apes	*Pongo*
Lemuridae	x							
Cebidae		x	x					
Atelidae		x	x	x	x			
Cercopithecidae			x	x	x			
Lorisidae			x	x	x			
Hylobatidae						x	x	x
African apes						x	x	x
Pongo						x	x	x

Figure 14: IRUAFS multiple comparison between taxonomic groups (x denotes no significant mean difference, p<0.05)

The lorises, however, show no mean difference from the cercopithecoids and atelids at this level. The hominoid families exhibit no significant mean difference from one another.

TALOCRURAL JOINT

Lorisidae

The talar trochlea of *Nycticebus* has well defined lateral and medial crests, a sloping fibular malleolar facet, a steep tibial malleolar facet, and a variably defined groove for the tibia, sometimes fairly deep, in other specimens less deep. The medial crest curves round towards the talar head, suggesting a degree of wedging. These findings are mirrored in *Arctocebus*, although the few specimens studied reveal a more consistently well-defined trochlea groove. The talus of *Loris* has a more flattened trochlear groove, but is otherwise similar to other lorisid genera, with a high lateral crest and lower medial crest. The talus of *Perodicticus* is again like the other lorises, with very pronounced crests, a deep groove, and sloping fibular facet.

Lemuridae

The talus of *Varecia* has fairly well defined crests, with a steep medial facet, sloping fibular facet, and a very deeply and sharply grooved trochlea. The trochlea shows little obvious anteroposterior wedging.

Cebidae

The talus of *Saimiri* has very steep sided tibial and fibular facets with well-defined crests. A very pronounced groove is evident on the trochlea in some specimens, but a fairly shallow trochlea is seen in others. The trochlea also shows signs of slight wedging.

Atelidae

In *Chiropotes*, the talus has steep-sided tibial and fibular facets, quite marked wedging, and a relatively shallow groove on the trochlea. In *Alouatta*, the talus also has fairly steep malleolar facets, although in some specimens these become more sloping towards the anterior end of both crests. The trochlea has a relatively shallow groove, with substantial wedging in some specimens, and less in others.

Cercopithecidae

The talus of *Cercopithecus* has very high and distinct crests, with the lateral crest higher than the medial. A well-defined groove is evident on the trochlea. The medial crest veers out towards the talar head, suggesting a degree of wedging. The lateral malleolar facet is at an acute angle (converging underneath the trochlea) and the medial facet slightly sloping but generally steep. In *Macaca*, the talus again has very distinct crests, especially on the lateral side, and the lateral crest is markedly higher than the medial. The malleolar facets are almost vertical, with the lateral facet sometimes at an extremely acute angle like *Cercopithecus*. The talus has a very deep and sharply grooved trochlea, sometimes 'V' shaped.

Hylobatidae

Hylobates, like the cercopithecids, has steep sided malleolar facets on the talus (although less so on the medial side), sometimes retreating underneath the trochlea to form an acute angle on the lateral side, with extremely well defined crests on the trochlea. The trochlea is rather flattened, despite the pronounced crests and steep sides. The medial crest diverges out towards head, resulting in fairly pronounced wedging. The trochlear crests do not diverge gradually, however, but remain parallel or very slightly diverge, and then the medial crest diverges rapidly out toward the talar head.

Great apes

The *Gorilla* talus has a very steep lateral facet, and a sloping medial facet. Both facets become more sloping towards the neck and head. The trochlea is very flat, with poorly defined crests, although a couple of specimens have a quite distinct

lateral crest. The medial facet diverge out towards the head to form significant wedging. In *Pan*, the talus has a very well defined lateral crest, and a less prominent medial crest, with an acute angle formed between the lateral facet and the top of the trochlea. The trochlea groove is sometimes quite distinct, but curved rather than sheer. Other specimens are almost flat. In *Pongo*, the talus has well-defined crests, steep facets, and a fairly well defined groove. The lateral crest is particularly high compared to the medial side. The medial crest does not curve round towards head, but runs straight in to the line of the head and neck.

ITD

For the depth of the talar trochlea, the lorises again exhibit the highest mean values, suggesting a relatively deep talar trochlea (Table 14). *Loris* shows a distinctly higher value than any of the others, while the other lorisid genera show depths more comparable with the cercopithecids. The closest genera to the lorises are *Cercopithecus*, *Macaca*, and *Varecia*. *Gorilla*, *Pan* and *Hylobates* show the lowest values, indicative of a comparatively shallow trochlea, although all three genera show high degrees of variability. The New World monkey genera most closely resemble these hominoids. *Pongo* is apparently unique among the hominoids in exhibiting a deeper trochlear trough.

Most of the fossil taxa (*Dendropithecus*, *Limnopithecus*, *Proconsul* and *Rangwapithecus*) show means for this index that are greater than those of *Gorilla*, *Pan* and *Hylobates*, but less than *Pongo*, which would suggest they possess moderately shallow trochlea troughs. These taxa are overall intermediate between the ceboids and *Pongo*. *Kalepithecus*, however, is more like the cercopithecids in this feature, with a mean value falling in between *Macaca* and *Cercopithecus*.

The plot for this index clearly shows the high values attained for *Loris*, *Nycticebus* and *Arctocebus* in this index, although *Perodicticus* can barely be distinguished from the other taxa (Figure 15). Again, *Gorilla*, *Pan* and *Hylobates* represent the opposite extreme within the primate range to the lorisids, but *Pongo* is different from the other hominoids in this character. From the plot it is not easy to discern

the character states of the fossils from the other genera, as they are part of a cluster of taxa exhibiting an index of approximately 10.

Genus	Number	Mean	Range
Gorilla	20	5.011	0.858 - 8.092
Pan	20	5.669	1.048 - 10.459
Hylobates	20	5.860	1.634 - 10.434
Alouatta	17	6.277	3.444 - 8.615
Saimiri	20	6.907	4.521 - 10.573
Chiropotes	7	6.938	4.839 - 8.964
**Dendropithecus*	2	7.392	6.860 – 7.920
**Limnopithecus*	2	7.696	7.060 – 8.330
**Proconsul*	9	8.991	6.060 – 11.730
**Rangwapithecus*	2	9.441	8.700 – 10.190
Pongo	20	9.671	5.975 - 12.935
Varecia	9	10.061	6.349 - 12.596
Cercopithecus	20	10.232	8.061 - 12.205
**Kalepithecus*	3	10.405	8.510 – 12.500
Macaca	20	10.666	6.285 - 13.851
Perodicticus	19	11.117	5.814 - 16.067
Arctocebus	3	13.086	9.148 - 17.288
Nycticebus	11	13.464	7.823 - 18.792
Loris	4	19.250	13.281 - 23.183

Table 14: ITD means and ranges (fossils indicated by *)

The multiple comparison test for this index places the lorises at the opposite extreme of the primate range from the hominoids and the atelines, differing from these families at the 95% confidence level, but showing no apparent difference from the lemurids and cercopithecoids (Figure 17). The hylobatids are intermediate in their morphology between New World monkeys and the African apes, and the means between apes and New World primates exhibit no differences at the 95% confidence level. As suggested by the table of means and ranges, the fossil genera are intermediate between the New World monkeys and *Pongo*, but show no mean difference to *Pongo*, the lemurids and the cercopithecids, as well as to the cebids.

IAPTW1

For this index of trochlear wedging, the anterior and posterior breadths of the talar trochlea are compared directly, without taking into account the size of the trochlea. The lorises and *Varecia* show the lowest mean values, indicating less anteroposterior wedging of the talar trochlea, whilst the hominoids (most particularly *Gorilla*, *Pan* and *Hylobates*) show the highest mean values (Table 15). *Gorilla* is most extreme in its range of variation, with a maximum value of approximately 296. *Alouatta*, *Cercopithecus* and *Chiropotes*, however, are not much lower than *Pan* and *Hylobates*, and the maximum in the range of *Alouatta* is higher than that of *Pan*. *Pongo* is significantly lower than the other hominoids, comparable to *Saimiri* and *Macaca*.

Genus	Number	Mean	Range
Loris	4	107.204	80.157 - 123.684
Arctocebus	3	111.493	101.115 - 128.030
Nycticebus	11	113.294	82.033 - 137.857
Varecia	9	113.558	103.799 - 122.543
Perodicticus	19	115.812	81.408 - 134.505
Pongo	20	124.493	100.659 - 159.194
Saimiri	20	127.982	113.198 - 162.245
Macaca	20	129.432	100.787 - 161.463
Cercopithecus	20	141.598	120.448 - 166.271
Chiropotes	7	143.429	123.479 - 163.097
Alouatta	17	143.989	111.653 - 189.264
Pan	20	149.612	125.111 - 169.810
**Kalepithecus*	1	157.303	-
Hylobates	20	158.009	132.805 - 182.465
**Dendropithecus*	1	164.516	-
**Proconsul*	5	170.587	162.960 – 179.630
Gorilla	20	198.935	142.452 - 295.822

Table 15: IAPTW1 means and ranges (fossils indicated by *)

The fossil taxa exhibit fairly high values for this index, certainly falling within the range exhibited for the African apes and *Hylobates*. As single specimens, however, *Kalepithecus* and *Dendropithecus* are well within the range of many of the observed taxa. *Proconsul* shows a particularly high index, closer to *Gorilla* than any of the other extant hominoids.

The plot for this index clearly shows that *Gorilla*, *Hylobates*, *Pan* and the fossil taxa have higher means than all other taxa, with *Gorilla* showing the most extreme value and a very large range of variation (Figure 16). The diagram also shows, however, that *Hylobates*, *Pan* and the fossils fall within the range of variation for *Alouatta*, despite higher mean values. Interestingly, *Pongo* exhibits a mean lower than all of the New and Old World monkey taxa, verging on the results achieved for the strepsirhines. The lorises and *Varecia* clearly represent the opposite extreme from the African apes and *Hylobates*, uniformly showing means closer to 100, which signifies little difference between the anterior and posterior breadths of the trochlea. Indeed, three of the loris taxa (*Loris*, *Nycticebus* and *Perodicticus*) have range minimums that fall below 100, which would indicate very slight wedging in the opposite direction.

In the multiple comparison test the means for the fossil and extant apes, with the notable exception of *Pongo*, and lorises again fall at either ends of the primate range (Figure 18). The loris mean is no different from that of the lemurids at the 95% significance level, whilst the African apes are not dissimilar from those of the proconsulids and hylobatids. *Pongo* is intermediate between the monkeys and the strepsirhines in this index, showing no significant difference to the lemurids, cebids and cercopithecids. Both the lorises and the African apes differ considerably from the cercopithecoids and ceboids, but in different ways.

IAPTW2

This second index of trochlea wedging is derived from the difference between the anterior and posterior trochlear breadths, and divided by the length of the trochlea to give an estimate of wedging across the length of the trochlea. When calculated like this, *Gorilla* again has the highest mean value for this index, suggesting a comparatively high degree of anteroposterior trochlear wedging across its length, with *Hylobates* as the next highest.

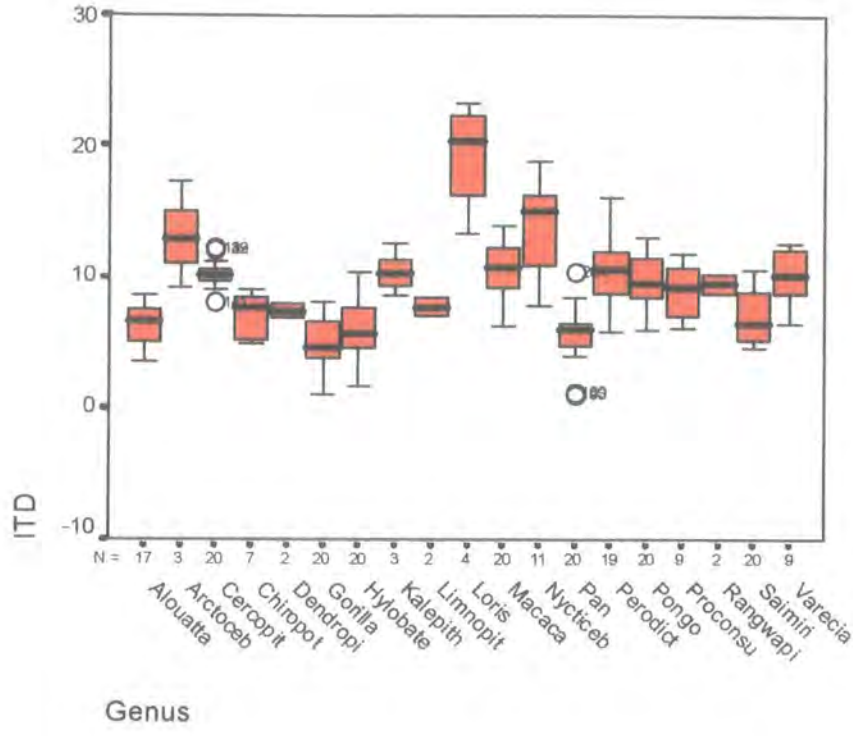

Figure 15: ITD boxplot showing means and ranges by genus

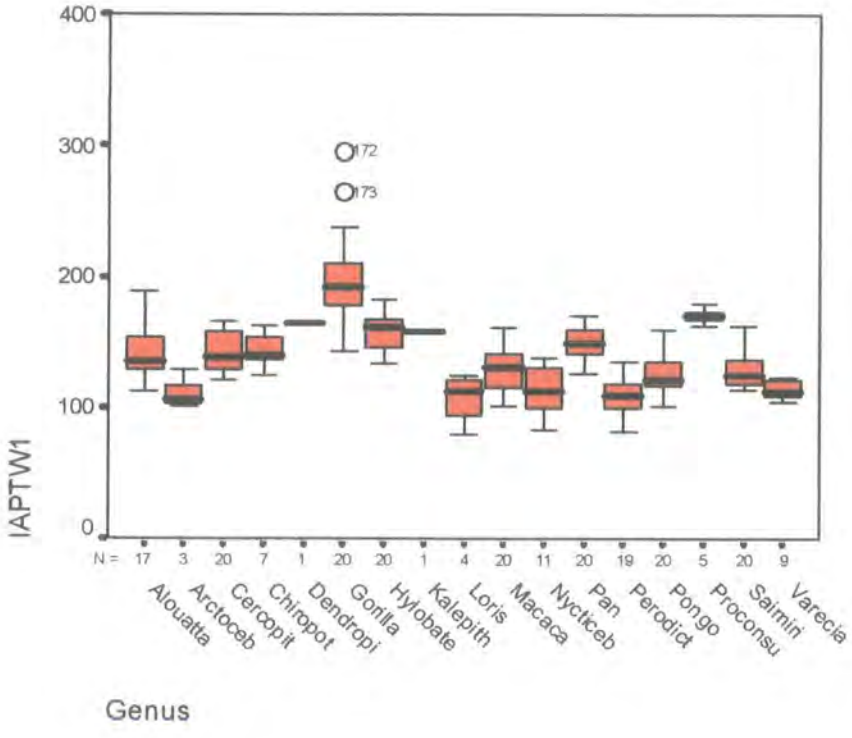

Figure 16: IAPTW1 boxplot showing means and ranges by genus

Taxonomic grouping	African apes	Hylobatidae	Atelidae	Cebidae	Proconsulidae	*Pongo*	Lemuridae	Cercopithecidae	Lorisidae
African apes	x	x	x	x					
Hylobatidae	x	x	x	x					
Atelidae	x	x	x	x					
Cebidae	x	x	x	x	x		x		
Proconsulidae				x	x	x	x	x	
Pongo					x	x	x	x	
Lemuridae				x	x	x	x	x	x
Cercopithecidae					x	x	x	x	x
Lorisidae							x	x	x

Figure 17: ITD multiple comparison between taxonomic groups (x denotes no significant mean difference, p<0.05)

Taxonomic grouping	Lorisidae	Lemuridae	*Pongo*	Cebidae	Cercopithecidae	Atelidae	Hylobatidae	Proconsulidae	African apes
Lorisidae	x	x							
Lemuridae	x	x	x						
Pongo		x	x	x	x				
Cebidae			x	x	x	x			
Cercopithecidae			x	x	x	x			
Atelidae				x	x	x	x		
Hylobatidae						x	x	x	x
Proconsulidae							x	x	x
African apes							x	x	x

Figure 18: IAPTW1 multiple comparison between taxonomic groups (x denotes no significant mean difference, p<0.05)

Pan, *Cercopithecus*, *Chiropotes* and *Alouatta* exhibit similar values, moderately less than that seen in *Hylobates* (Table 16). The lorises and *Varecia* are distinctly lower, at the opposite extreme to *Gorilla*. *Pongo* shows a very low value for this index, intermediate between the lorisids and *Saimiri*.

The fossil taxa all exhibit very high mean values for the second index of trochlear wedging, comparable to (or exceeding that of) *Gorilla*. This would suggest that they all have significant wedging relative to overall trochlea length. It may be the case, however, that these results are distorted by extreme individuals, as may be seen in the two *Kalepithecus* specimens, which vary considerably in their values (32.900 and 94.580).

Genus	Number	Mean	Range
Loris	4	3.117	-17.195 - 15.222
Nycticebus	11	6.530	-12.925 - 18.772
Arctocebus	3	6.948	0.714 - 16.629
Varecia	9	7.144	2.066 - 12.450
Perodicticus	19	7.780	-13.239 - 15.953
Pongo	20	12.948	0.374 - 31.711
Saimiri	20	14.634	7.222 - 26.483
Macaca	20	15.162	0.524 - 26.843
Cercopithecus	20	21.898	13.309 - 33.031
Pan	20	22.080	12.951 - 28.399
Alouatta	17	23.919	7.446 - 42.143
Chiropotes	7	24.926	15.366 - 34.913
Hylobates	20	26.159	17.190 - 35.101
**Dendropithecus*	1	38.217	-
**Proconsul*	5	38.682	33.330 – 42.370
Gorilla	20	38.838	20.403 - 56.800
**Kalepithecus*	2	63.741	32.900 – 94.580
**Rangwapithecus*	1	86.705	-

Table 16: IAPTW2 means and ranges (fossils indicated by *)

The plot for this index again shows that lorises have a low degree of anteroposterior wedging, with the negative figures indicating the element of posterioanterior wedging found in these specimens (Figure 19). It is only *Gorilla* of the extant genera, and to a lesser extent *Hylobates*, however, that shows any distinct difference from the remaining taxa, with *Pan* falling more within the monkey range than its hominoid counterparts in this feature. *Pongo* again has a

relatively low mean value for this index, which may also be skewed by the presence of an apparent outlier. The fossils are visibly high in this index; *Kalepithecus* and *Rangwapithecus* in particular are very extreme compared to the extant forms.

This index of trochlear wedging is comparable in its results to the previous index in the multiple comparison test, with the African apes exhibiting similar character states to both the atelids and the hylobatids at the 95% confidence level (Figure 21). This particular analysis, however, did indicate a comparative difference between the New World families. As with the previous analysis, the strepsirhines form a group that was significantly different to all of the other divisions at 95% confidence, with the exception of *Pongo*, which cannot be distinguished from the lemurids. The fossil genera are most extreme, at the opposite end of the character range from the lorisids, but overlap with the African apes, hylobatids and atelids at the 95% confidence level.

SUBTALAR JOINT

Lorisidae

The posterior calcaneal facet in all of the lorises is short and relatively shallow, but well defined, and thus the depth of curvature of the facet is expected to be fairly low. The major difficulty experienced with these smaller taxa is with the depth callipers, where the end of the gauge is wider than the maximum depth point of the talus. The depth in these specimens was estimated. The orientation of the posterior calcaneal facet is highly varied in these genera, ranging from almost parallel to the lateral crest (particularly in some of the *Perodicticus* specimens) to fairly oblique.

Lemuridae

The posterior calcaneal facet of *Varecia* is also short, but comparatively deep, forming a well defined receptive cup for the facet on the calcaneus. The orientation of the long axis of curvature is generally moderately oblique.

Cebidae

The *Saimiri* posterior calcaneal facet is generally fairly short, well curved and relatively deep. The orientation is often close to parallel with the lateral crest, indicating a sub-talar axis more perpendicular to the long axis of the foot, but this is highly varied.

Atelidae

The posterior calcaneal facet of the atelids is relatively shallow, and widely curving. As with *Saimiri*, the orientation varied greatly, ranging from almost parallel with the lateral crest to quite oblique.

Cercopithecidae

The posterior calcaneal facet in both *Cercopithecus* and *Macaca* is relatively short and deep, and more steeply curved than the other taxa, forming a well defined receptive socket for the opposite convex facet on the calcaneus. In most specimens this facet adjoins the neighbouring anterior facet. Again the orientation varies considerably, but generally lies oblique to the long axis of the foot.

Hylobatidae

The *Hylobates* posterior calcaneal facet is also seemingly tightly curved, representing a fairly deep articulation. This facet is orientated in an oblique axis to the long axis of the foot.

African apes

In the African apes, the posterior calcaneal facet is long, broad, and widely curving, although this varies across genera, and especially within *Pongo*. It is also completely isolated from the other calcaneal facets. The obliquity of the facet is extremely variable, but mainly positioned at an angle to the lateral crest.

IPCFD

For the index of depth of the posterior calcaneal facet, the highest values are found in *Cercopithecus* and *Macaca*, indicating a steeply curved facet (Table 17). *Varecia* and *Pan* show very similar mean values to each other for this feature, which (surprisingly) are only moderately less than the cercopithecids. The lowest values are seen in *Nycticebus*, *Alouatta*, *Loris* and *Perodicticus*, suggesting relatively wide and shallow curvature in these genera. *Pongo*, *Gorilla* and *Hylobates* fall in the middle of the primate range, comparable to *Saimiri*. The fossil genera vary in this characteristic; *Limnopithecus* and *Rangwapithecus* have a relatively shallowly curved articulation and, at the other end of the spectrum, *Proconsul* and *Kalepithecus* exhibit a facet that is relatively deeper. *Dendropithecus* is intermediate in this feature, falling in the middle of the primate range of variation.

Genus	Number	Mean	Range
Nycticebus	11	11.622	6.143 - 15.730
Alouatta	17	13.824	10.345 - 18.065
Loris	4	14.285	10.933 - 15.842
Perodicticus	17	15.575	9.548 - 24.011
**Limnopithecus*	1	16.346	-
Chiropotes	7	16.412	14.475 - 19.241
**Rangwapithecus*	1	16.418	-
Arctocebus	3	16.591	11.069 - 22.101
**Dendropithecus*	2	17.170	16.950 – 17.390
Pongo	20	17.933	9.716 - 24.521
Hylobates	20	19.004	10.035 - 24.074
Saimiri	20	19.026	13.036 - 25.845
**Proconsul*	7	19.565	14.890 – 23.790
Gorilla	20	20.672	16.508 - 29.229
**Kalepithecus*	2	20.769	17.090 – 24.440
Pan	20	22.302	16.043 - 28.171
Varecia	9	22.743	18.543 - 25.383
Macaca	20	25.864	18.266 - 32.892
Cercopithecus	20	26.500	21.598 - 32.024

Table 17: IPCFD means and ranges (fossils indicated by *)

The plot illustrates these findings (Figure 20). The results for this variable show few discernable patterns between the lorises and hominoids, in terms of similarity or extreme difference, although the lorisids tend to be at the lower end of the

primate range for this index and the hominoids vary considerably, but generally towards the higher index value. What is particularly evident from the plot is the huge variability across all of the genera

The multiple comparison test results for this index illustrate the variable nature of this characteristic (Figure 22). The lorisids and atelines show no significant difference to one another at the lower end of the scale, but differ from all other genera at the 95% confidence level. At the opposite extreme, the cercopithecids are unique in their uniformly high index. The other taxa overlap considerably with each other, and the hominoids show no apparent uniformity. The African apes are towards the cercopithecid end of the range, *Pongo* is more loris-like, and *Hylobates* occupies an intermediate position. The proconsulids show no significant difference to any of the intermediate taxa.

ASTA-LC

Among the extant genera, the angle of the subtalar axis did not reveal any dramatic grouping, as the results show a steady gradient of means within a range of 62° – 78.5° (Table 18). The lowest mean values are obtained for *Nycticebus* and the African apes, indicating an oblique subtalar axis relative to the lateral crest and the long axis of the foot. Relatively low values are also seen in the cercopithecids, *Loris*, *Pongo* and *Hylobates*. The highest means and upper range limits are found among the ceboids, *Arctocebus*, *Perodicticus* and *Varecia*, suggesting subtalar axes approximating perpendicular to the longitudinal axis of the foot in these genera. Although the results suggest particular character states for the African apes, ceboids and cercopithecids, the lorisids are quite varied in this feature within their family grouping, representing both the lowest and second highest values.

The fossil genera are fairly uniform in this particular character, falling at the lower end of the primate range, similar to the African apes. This would suggest that these genera possess a comparatively oblique subtalar axis, indicative of enhanced accessory movement at this point.

Genus	Number	Mean	Range
**Rangwapithecus*	1	56.000	-
Nycticebus	11	62.000	51.000 – 83.000
**Proconsul*	9	63.667	55.000 – 69.000
Pan	20	64.000	56.000 - 73.000
**Kalepithecus*	2	64.500	63.000 – 66.000
**Limnopithecus*	1	65.000	-
**Dendropithecus*	2	65.500	62.000 – 69.000
Gorilla	20	66.850	56.000 – 79.000
Macaca	20	67.950	59.000 - 77.000
Loris	4	68.250	64.000 – 77.000
Cercopithecus	20	68.800	53.000 - 78.000
Pongo	20	69.150	57.000 – 81.000
Hylobates	20	70.632	59.000 - 86.000
Varecia	9	71.444	62.000 – 88.000
Chiropotes	7	72.714	69.000 - 77.000
Arctocebus	3	73.333	68.000 – 82.000
Saimiri	20	75.526	70.000 - 84.000
Perodicticus	17	76.444	62.000 - 87.000
Alouatta	17	78.357	71.000 – 88.000

Table 18: ASTA-LC means and ranges (fossils indicated by *)

The plot (Figure 23) shows the large ranges exhibited by many of the genera, and the particularly high upper limits (approaching 90°) of *Alouatta*, *Hylobates*, *Perodicitcus* and *Varecia*. This indicates a subtalar axis perpendicular to the longitudinal axis of the foot. All of the fossil genera are clearly seen to have means and ranges at the lower end of the primate range for this index.

The multiple comparison test (Figure 24) illustrates the huge amount of overlap between the groups studied, probably due to the extensive ranges seen in many taxa, and identifies two different groups of primates in this characteristic. The atelids and cebids have a clearly different morphology from the great apes, cercopithecoids and proconsulids, with subtalar axes approaching 90°. The latter three families have more oblique subtalar axes. There is, however, a certain amount of overlap between these two extremes, seen in the strepsirhine genera and *Hylobates*.

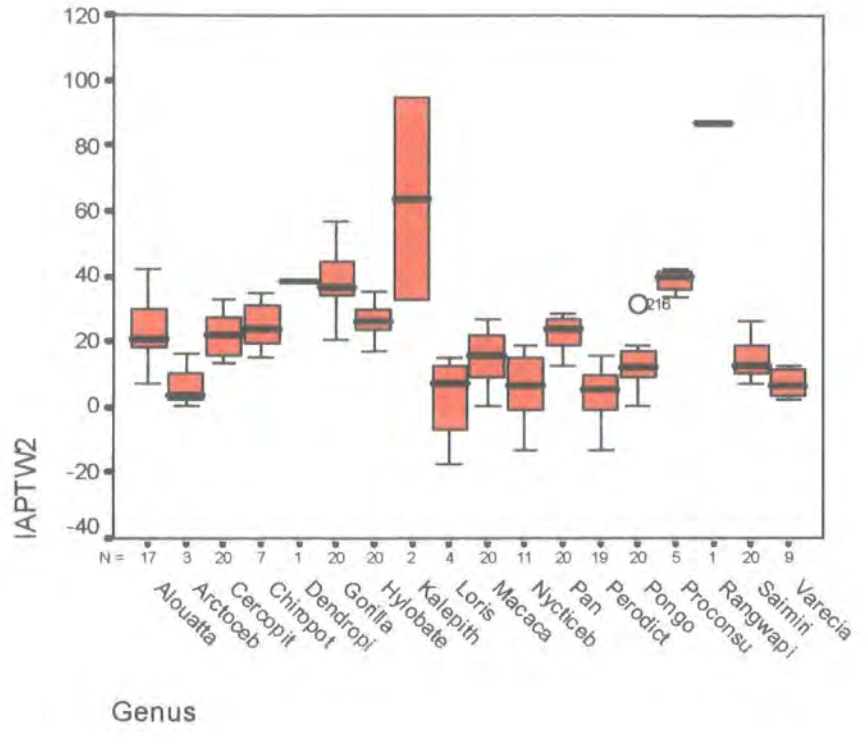

Figure 19: IAPTW2 boxplot showing means and ranges by genus

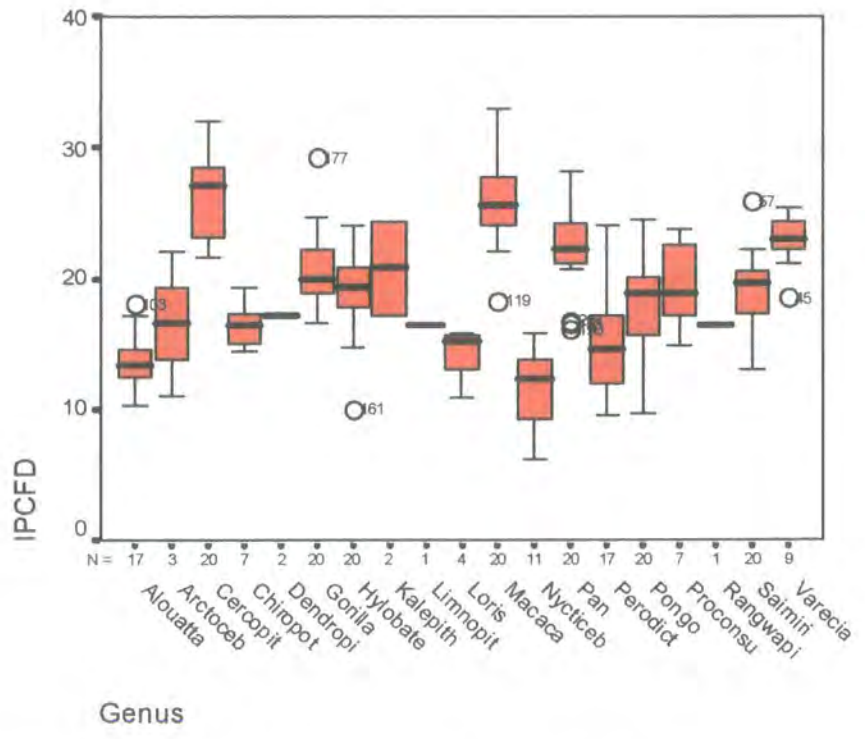

Figure 20: IPCFD boxplot showing means and ranges by genus

Taxonomic grouping	Lorisidae	Lemuridae	*Pongo*	Cebidae	Cercopithecidae	Atelidae	Hylobatidae	African apes	Proconsulidae
Lorisidae	x	x							
Lemuridae	x	x	x						
Pongo									
Cebidae			x	x	x				
Cercopithecidae			x	x	x	x			
Atelidae					x	x	x	x	x
Hylobatidae						x	x	x	x
African apes						x	x	x	x
Proconsulidae					x	x	x	x	x

Figure 21: IAPTW2 multiple comparison between taxonomic groups (x denotes no significant mean difference, p<0.05)

Taxonomic grouping	Lorisidae	Atelidae	*Pongo*	Proconsulidae	Hylobatidae	Cebidae	African apes	Lemuridae	Cercopithecidae
Lorisidae	x	x							
Atelidae	x	x							
Pongo			x	x	x	x			
Proconsulidae			x	x	x	x	x	x	
Hylobatidae			x	x	x	x	x		
Cebidae			x	x	x		x		
African apes				x	x	x	x	x	
Lemuridae				x			x	x	
Cercopithecidae									x

Figure 22: IPCFD multiple comparison between taxonomic groups (x denotes no significant mean difference, p<0.05)

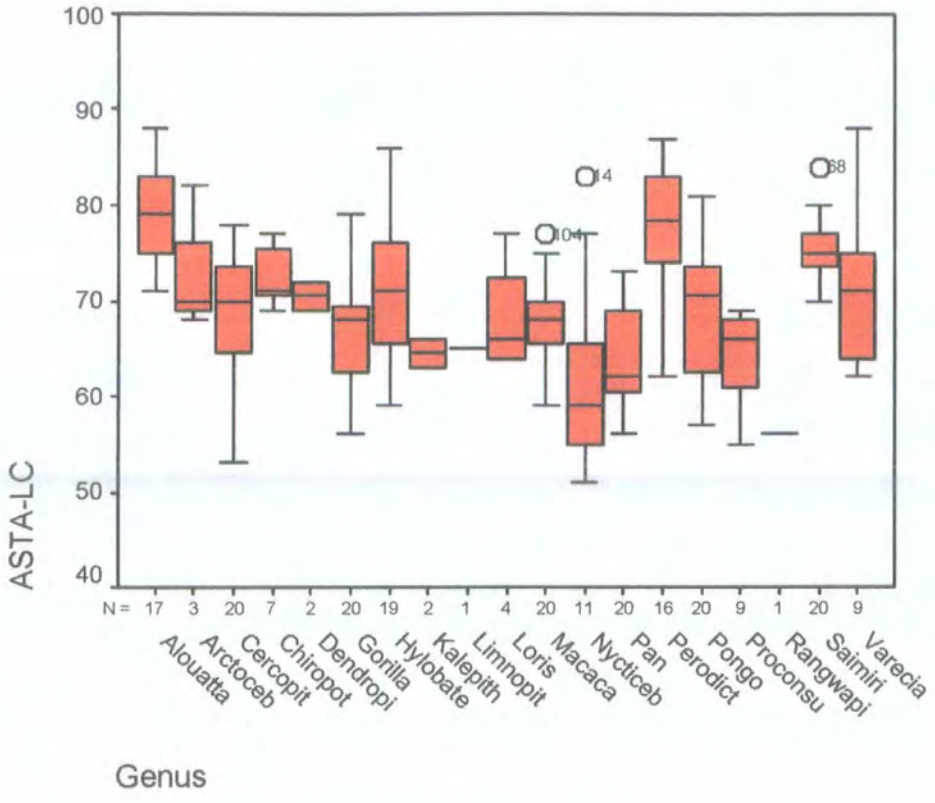

Figure 23: ASTA-LC boxplot showing means and ranges by genus

Taxonomic grouping	Proconsulidae	African apes	Cercopithecidae	*Pongo*	Hylobatidae	Lorisoidae	Lemuridae	Cebidae	Atelidae
Proconsulidae	x	x	x	x	x	x	x		
African apes	x	x	x	x	x	x	x		
Cercopithecidae	x	x	x	x	x	x	x		
Pongo	x	x	x	x	x	x	x		
Hylobatidae	x	x	x	x	x	x	x	x	x
Lorisidae	x	x	x	x	x	x	x	x	x
Lemuridae	x	x	x	x	x	x	x	x	x
Cebidae					x	x	x	x	x
Atelidae					x	x	x	x	x

Figure 24: ASTA-LC multiple comparison between taxonomic groups (x denotes no significant mean difference, $p<0.05$)

TALAR HEAD AND NECK

Lorisidae

Lorises are quite similar in their talar head and neck characteristics, but highly variable within genera. The have relatively long and slender talar necks, most particularly *Loris* and *Arctocebus*, and a seemingly very flat head. The medial crest of the trochlea curves round into the line of the head and neck.

Lemuridae

Similarly, *Varecia* has a long talar neck in comparison to the trochlea, but the neck is more cylindrical than in the lorisid talus, and the head more ball-like.

Cebidae

Saimiri has a distinctly long talar neck, with a spherical head, but the neck is less robust than in the strepsirhines. The shaft tapers towards the body of the talus.

Atelidae

The talar neck of *Chiropotes* is also relatively thin and very long, with a spherical head. In contrast, *Alouatta* has a talus that seems altogether very flat and wide, and this is reflected in the features of the neck and head. The talar neck is also comparatively shorter in some specimens, and the talar head is more in line with the trochlea.

Cercopithecidae

The *Cercopithecus* specimens seem fairly conservative in their talar neck length, and the head is quite large and 'ball-like'. Similarly, *Macaca* has a medium length talar neck, although the neck is found to be particularly wide relative to the head. The head is also flatter than that of *Cercopithecus*.

Hylobatidae

The *Hylobates* talus neck is comparatively short and flat, but is combined with a rather spherical head.

Great apes

The great apes are divided in their talar head and neck features, with the African apes showing very different features to *Pongo*. The talus of *Gorilla* is characterised by a short, stubby talar neck, with a large, and sometimes quite flat, head. In some specimens, the neck is so short that the head ostensibly extends from the body of the talus. In *Pan*, the talar neck is also short and the head large, but to a lesser extent than in *Gorilla*. In contrast, *Pongo* has a fairly long talar neck, and a smaller more spherical head (although a couple of the specimens have distinctly flattened heads).

ITHB1

For the first index of talar head breadth, the mediolateral breadth of the head is measured relative to the breadth of the trochlea. A high index reflects a broad talar head relative to the overall structure of the body of the talus. The highest mean value for this index is found in *Nycticebus* with the next highest values in *Perodicticus, Gorilla*, *Pan*, *Loris* and *Hylobates* (Table 19). The mean value for *Arctocebus* is much lower than for the other lorises, and *Pongo* has the second lowest mean value overall.

On the whole there seems to be a distinct division between the extant forms in this characteristic, with no intermediary forms. The strepsirhine and hominoid grouping (to the exclusion of *Pongo*) all have mean indices above 127, indicating a large area for excursion at the talonavicular articulation, whilst the remaining genera all fall below 114. It must be noted, however, that most of the taxa have very large ranges of variation.

The fossil genera, to a certain extent, bridge the gap between the two morphologies. At the lower end of the range, *Dendropithecus* and *Kalepithecus*

exhibit talar head breadths equivalent to *Saimiri* at the higher end of this grouping. *Limnopithecus*, on the other hand, falls towards the bottom end of the higher range, with a similar index value to *Arctocebus*. The other fossil genera (*Rangwapithecus* and *Proconsul*) show mean indices between these two extremes, but ranges that overlap both.

Genus	Number	Mean	Range
Chiropotes	7	104.529	94.187 - 109.221
Pongo	20	104.961	89.948 - 128.595
Alouatta	17	108.550	97.333 - 123.725
Cercopithecus	20	110.775	97.530 - 124.623
Macaca	20	111.486	95.846 - 136.706
**Dendropithecus*	1	112.745	-
Saimiri	20	113.137	96.796 - 127.390
**Kalepithecus*	1	113.542	-
**Rangwapithecus*	3	118.753	114.820 – 120.79
**Proconsul*	9	121.174	102.330 – 155.460
Arctocebus	3	127.033	117.035 - 145.421
**Limnopithecus*	2	127.467	118.820 – 136.110
Varecia	9	133.445	117.537 - 147.735
Hylobates	20	137.359	104.207 - 171.736
Loris	4	138.447	129.969 - 145.675
Pan	20	138.928	125.955 - 164.221
Gorilla	20	143.671	67.518 - 179.449
Perodicticus	18	143.784	116.129 - 180.556
Nycticebus	11	156.793	133.030 - 200.678

Table 19: ITHB1 means and ranges (fossils indicated by *)

The plot for this variable clearly shows the different morphology of the hominoid and loris genera (with the exclusion of *Pongo*). A *Gorilla* outlier, however, may have reduced its overall mean considerably, as the high outlying value of *Nycticebus* may radically skew its mean (Figure 25). The closest taxon to this group is *Varecia*. *Pongo* is apparently more like the New and Old World monkeys in this feature, exhibiting a comparatively narrow talar head.

The multiple comparison test shows the lemurids, lorisids, hylobatids and African apes to have means that were not different to one another at the 95% confidence level, with the lemurid sample overlapping with the Cebidae and Cercopithecidae (Figure 27). The Lorisidae have the highest extreme in this talar breadth index.

The remaining families of the Old and New world monkeys, and *Pongo*, differ from the Lorisidae and the other hominoids at the 95% confidence level, but are indistinguishable from one another. *Pongo* and the atelids are at the lower extreme in this index. The proconsulids, as revealed above, occupy an intermediate position, and show no significant mean difference from the cercopithecids, cebids and lemurids at the 95% confidence level. They do not, however, show similarity to the groups on either extreme.

ITHB2

This second measure of talar head breadth is achieved by comparing the breadth and height of the head. A high index suggests a more flattened talar head in comparison to the relatively spherical nature of those represented by lower indices. The means for the hominoids and the lorises are all higher than those found in the remaining genera, indicating a mediolaterally broad and flat talar head in the Hominoidea and Lorisoidea (Table 20). The lorises exhibit the flattest talar head comparatively.

Most of the the fossil genera are relatively uniform in this index, with *Proconsul*, *Rangwapithecus*, *Kalepithecus* and *Dendropithecus* showing indices comparable to *Cercopithecus* and *Saimiri* at the lower end of the primate range. *Limnopithecus*, on the other hand falls within the hominoid range with a higher index than the other fossil genera, and thus a flatter talar head. As a single specimen, however, the value does fall within the range for *Cercopithecus*, and thus cannot ultimately be considered different from the other fossils in this respect.

The plot highlights the uniformly high mean values for the lorises very well, and to a lesser extent those of the hominoids (Figure 26). Again, the outlying value of *Gorilla* may have skewed the diagram to a certain extent, and it is evident that a huge range of variation is found within this genus. The fossil genera clearly fall within the more conservative ranges of the monkey genera, with only *Limnopithecus* exhibiting a value close to the hominoids.

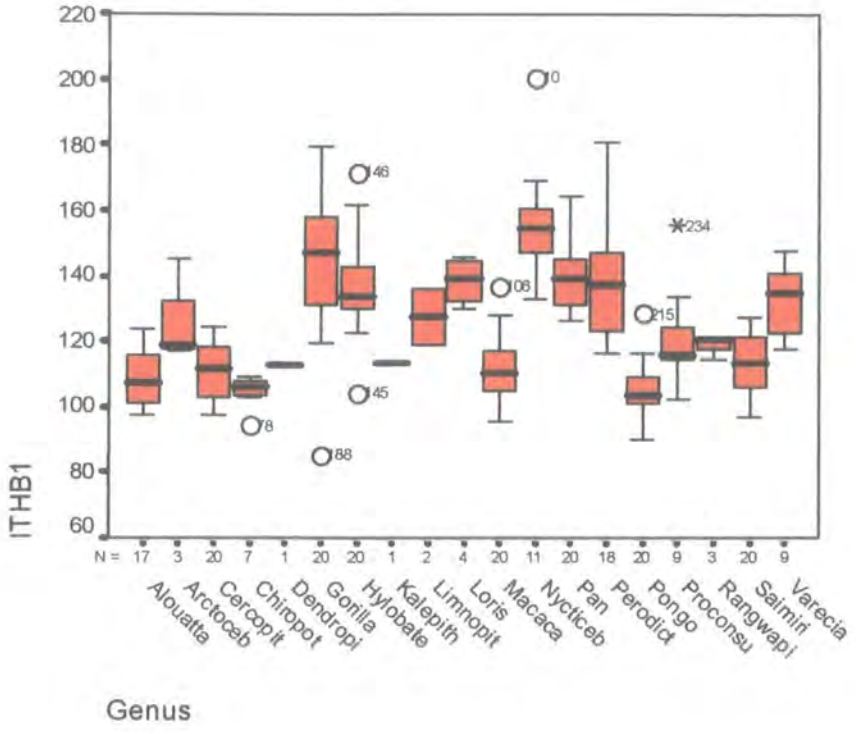

Figure 25: ITHB1 boxplot showing means and ranges by genus

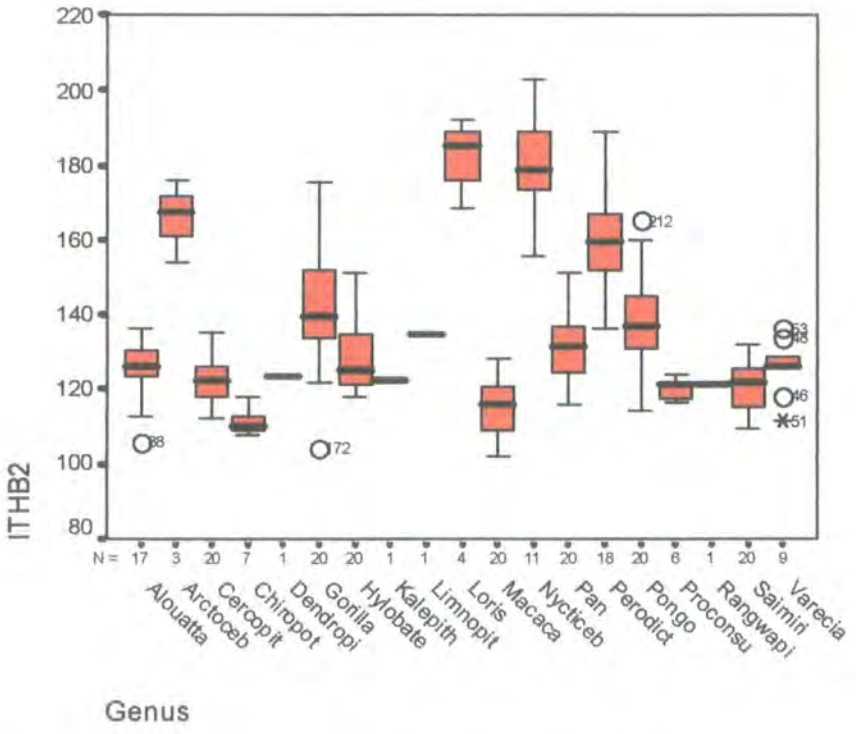

Figure 26: ITHB2 boxplot showing means and ranges by genus

Taxonomic grouping	*Pongo*	Atelidae	Cercopithecidae	Cebidae	Proconsulidae	Lemuridae	Hylobatidae	African apes	Lorisidae
Pongo	x	x	x	x					
Atelidae	x	x	x	x					
Cercopithecidae	x	x	x	x	x				
Cebidae	x	x	x	x	x				
Proconsulidae			x	x	x	x			
Lemuridae			x	x	x	x			
Hylobatidae						x	x	x	x
African apes						x	x	x	x
Lorisidae						x	x	x	x

Figure 27: ITHB1 multiple comparison between taxonomic groups (x denotes no significant mean difference, p<0.05)

Taxonomic grouping	Cercopithecidae	Cebidae	Atelidae	Proconsulidae	Lemuridae	Hylobatidae	African apes	*Pongo*	Lorisidae
Cercopithecidae	x	x	x	x	x				
Cebidae	x	x	x	x	x	x			
Atelidae	x	x	x	x	x	x			
Proconsulidae	x	x	x	x	x	x			
Lemuridae	x	x	x	x	x	x			
Hylobatidae		x	x	x	x	x	x	x	
African apes					x	x	x	x	
Pongo						x	x	x	
Lorisidae									x

Figure 28: ITHB2 multiple comparison between taxonomic groups (x denotes no significant mean difference, p<0.05)

Genus	Number	Mean	Range
Chiropotes	7	111.358	107.634 - 118.058
Macaca	20	114.823	102.206 - 128.488
Saimiri	20	120.100	109.701 - 132.172
**Proconsul*	6	120.310	116.400 – 124.110
**Rangwapithecus*	1	121.569	-
**Kalepithecus*	1	122.472	-
Cercopithecus	20	122.697	112.233 - 135.101
**Dendropithecus*	1	123.656	-
Alouatta	17	125.852	105.752 - 136.340
Varecia	9	125.883	111.404 - 136.210
Hylobates	20	128.746	117.930 - 151.267
**Limnopithecus*	1	134.667	-
Pongo	20	138.991	114.185 - 165.264
Gorilla	20	141.103	104.264 - 175.533
Pan	20	143.154	116.196 – 151.580
Perodicticus	18	161.025	136.275 - 189.024
Arctocebus	3	165.842	154.185 - 175.829
Nycticebus	11	179.904	155.667 - 202.622
Loris	4	182.660	168.651 - 192.147

Table 20: ITHB2 means and ranges (fossils indicated by *)

In the multiple comparison test, the Lorisidae differ from all of the other families at the 95% confidence level, but are most similar to the African apes, *Pongo* and Hylobatidae, at the opposite end of the primate range to the Old and New World monkeys (Figure 28). The great apes show no mean difference from the hylobatids at 95% confidence, but differ from all other taxa. The hylobatids occupy a fairly intermediate position in this analysis, also exhibiting no mean difference from the cebids, atelids and lemurids at this level.

The fossil genera have a morphology most consistent with the cercopithecids, cebids, atelids and lemurids in this analysis, revealing no significant mean difference to these families, as well as to *Hylobates* at the 95% confidence level.

ITHNL

The lowest mean values for this index, indicating a relatively short talar head and neck in relation to the talar body, are found in *Pan* and *Gorilla* (Table 21), but interestingly all of the hominoids and lorises show lower values than the other taxa. The cercopithecids and *Varecia* appear intermediate in this characteristic,

whilst the New World genera all exhibit a comparatively high index for this feature.

The fossil genera exhibit quite varied values for this index. The *Proconsul* mean value falls within the range of means of the extant hominoids, most similar to *Hylobates*, whilst the values for *Kalepithecus* are more consistent with the New World forms. The *Dendropithecus* specimen is more intermediate in this index, but consistant with the values achieved for *Loris* and *Arctocebus*. This would suggest that the *Proconsul* specimens has relatively short talar head and neck structures, similar to the extant hominoids in this feature. *Kalepithecus*, on the other hand, is characterised by elongation of this structure. The few specimens examined for *Kalepithecus* and *Dendropithecus*, however, fall within the limits of all of the extant taxa except the African apes.

Genus	Number	Mean	Range
Gorilla	20	39.074	29.522 - 48.798
Pan	20	42.699	33.726 - 51.698
Perodicticus	18	50.254	38.689 - 79.050
**Proconsul*	5	52.558	39.570 – 63.330
Hylobates	20	53.319	42.697 - 75.175
Nycticebus	11	54.903	38.663 - 83.000
Pongo	20	56.211	44.142 - 67.888
Arctocebus	3	57.704	53.333 - 61.573
**Dendropithecus*	1	60.510	-
Loris	4	61.243	49.351 - 72.304
Macaca	20	62.021	49.973 - 81.526
Varecia	9	63.659	43.043 - 73.424
Cercopithecus	20	66.224	50.578 - 83.218
Alouatta	17	69.082	51.977 - 90.923
**Kalepithecus*	2	72.639	71.080 – 74.190
Saimiri	20	74.016	59.889 - 99.248
Chiropotes	7	74.174	56.210 - 89.082

Table 21: ITHNL means and ranges (fossils indicated by *)

The apparently grouped nature of the hominoids and lorises in this feature is less evident on the plot (Figure 29), where *Loris* appears comparable to *Macaca*, although the more extreme characteristics of *Gorilla* and *Pan* are clearly shown. The *Proconsul* affinity with the African apes and lorises in this index is very clear, and the lower limits of the sample for this genus are visibly below those of

any of the monkey genera. *Kalepithecus* is also clearly seen to be within the ranges of the New and Old World monkeys, whilst the single *Dendropithecus* specimen shows no apparent specialisation.

The multiple comparison test shows two quite well-defined groups in this characteristic, with the hominoids and lorises at the lower extreme and the monkeys at the opposite end (Figure 31). The lemurids exhibit a somewhat intermediate status. The African apes are different to all other groups at the 95% confidence level. The hylobatids, however, exhibit similarities to both of the strepsirhine groups and *Pongo* at this level. The lorises fall within the hominoid group overall, showing no mean difference to the hylobatids and *Pongo* at the 95% confidence level.

The fossil genera are clearly shown to be intermediate in this index, showing no difference to any of the extant taxa at the 95% confidence level. This diagram, however, does not illustrate the apparent differences among the fossil genera and their respective similarities with the extant divisions.

ATH-LC

For the angle of the talar head to the lateral crest, the extant genera again seem to be divided into two distinct groups for their means; the lorises, hominoids, *Chiropotes* and *Saimiri* all fall above 35, whilst the other genera have means below 31 (Table 22). It must be noted, however, that a huge amount of variation is evident in most genera. The highest mean values are seen in *Nycticebus*, *Gorilla*, *Pan* and *Perodicticus*, indicating a much higher medial deviation of the talar head and neck from the direction of forward motion, which in turn would have implications for the mid-tarsal articulation. *Hylobates*, and more particularly *Pongo*, are somewhat lower than the other hominoids in their mean values for this feature, and *Loris* shows a value similar to *Hylobates*. Unfortunately, a value for *Arctocebus* was not obtained for this character. The angle found in *Cercopithecus* is comparatively much lower than all of the other taxa, although the angle suggests that the talus is still orientated medially from the long axis of the foot.

Genus	Number	Mean	Range
**Kalepithecus*	2	18.500	10.000 – 27.000
Cercopithecus	20	23.350	16.000 - 32.000
**Rangwapithecus*	3	25.333	16.000 – 35.000
**Proconsul*	9	27.667	20.000 – 36.000
Alouatta	17	30.143	16.000 - 43.000
Varecia	9	30.667	25.000 - 38.000
Macaca	20	31.000	18.000 - 42.000
**Limnopithecus*	1	31.000	-
Pongo	20	35.150	25.000 - 47.000
Chiropotes	7	35.286	30.000 - 43.000
Loris	4	36.000	36.000 - 36.000
Hylobates	20	36.105	14.000 - 53.000
Saimiri	20	36.316	29.000 - 43.000
Perodicticus	18	37.444	20.000 - 50.000
Pan	20	41.600	26.000 - 54.000
**Dendropithecus*	1	44.000	-
Gorilla	20	44.100	17.000 - 58.000
Nycticebus	11	45.000	36.000 - 60.000

Table 22: ATH-LC means and ranges (fossils indicated by *)

The fossil taxa generally fall within the primate group that exhibits more moderate medial torsion of the talar head and neck, with the exception of *Dendropithecus*, which is comparable with *Gorilla* in this character. *Kalepithecus*, *Rangwapithecus* and *Proconsul* (in particular) show talar head projection angles at the lower end of the primate range, comparable with (or more extreme than) that seen in *Cercopithecus*.

The plot highlights the large angle between the talar head and the lateral crest in *Gorilla*, *Pan* and *Nycticebus*, and the comparatively high index of the *Dendropithecus* specimen (Figure 30). *Cercopithecus* is different to all of the other extant taxa in its comparatively low angle between the orientations of these two talar features, matched only by the fossil forms. What is clear from this plot is that many of the genera have very large ranges of variation.

The multiple comparison test illustrates the huge amount of overlap between the families in this characteristic (Figure 32). The only real distinctions can be made between the cercopithecids and African apes, which are at opposite extremes in

this feature. The closest to the African apes are the lorisids, and the other apes are somewhat intermediate in this character. The fossil genera are most similar to the cercopithecoids, although they show no mean difference to the lemurids, atelids, *Pongo* amd hylobatids.

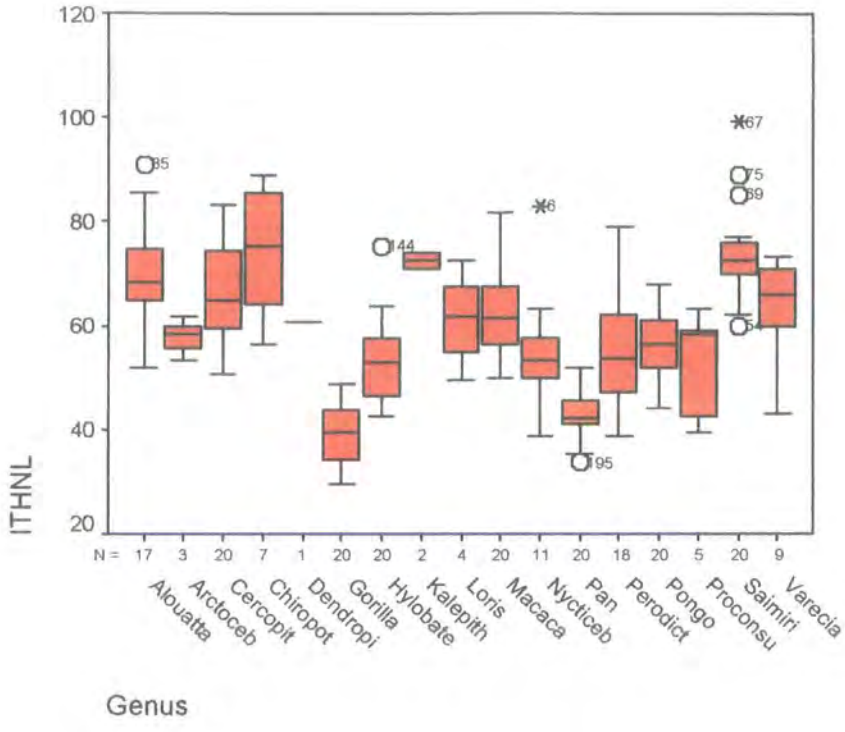

Figure 29: ITHNL boxplot showing means and ranges by genus

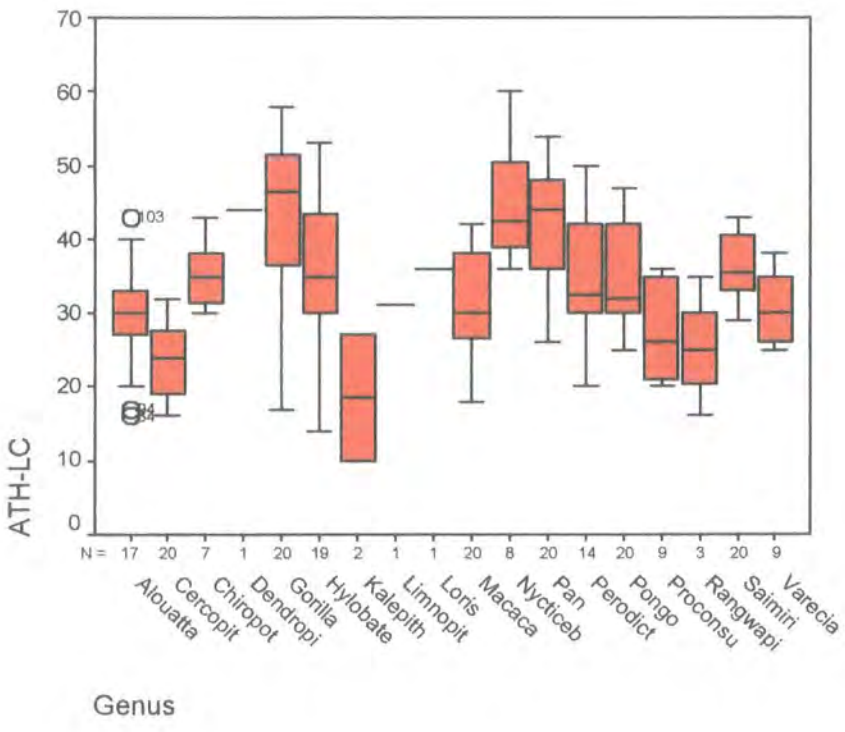

Figure 30: ATH-LC boxplot showing means and ranges by genus

Taxonomic grouping	African apes	Hylobatidae	Lorisidae	*Pongo*	Proconsulidae	Lemuridae	Cercopithecidae	Atelidae	Cebidae
African apes	x				x				
Hylobatidae		x	x	x	x	x			
Lorisidae		x	x	x	x	x			
Pongo		x	x	x	x	x			
Proconsulidae	x	x	x	x	x	x	x	x	x
Lemuridae		x	x	x	x	x	x	x	x
Cercopithecidae					x	x	x	x	
Atelidae					x	x	x	x	x
Cebidae					x	x		x	x

Figure 31: ITHNL multiple comparison between taxonomic groups (x denotes no significant mean difference, p<0.05)

Taxonomic grouping	Cercopithecidae	Proconsulidae	Lemuridae	Atelidae	*Pongo*	Hylobatidae	Cebidae	Lorisidae	African apes
Cercopithecidae	x	x	x	x					
Proconsulidae	x	x	x	x	x	x			
Lemuridae	x	x	x	x	x	x	x	x	
Atelidae	x	x	x	x	x	x	x	x	
Pongo		x	x	x	x	x	x	x	
Hylobatidae		x	x	x	x	x	x	x	x
Cebidae			x	x	x	x	x	x	
Lorisidae			x	x	x	x	x	x	x
African apes						x		x	x

Figure 32: ATH-LC multiple comparison between taxonomic groups (x denotes no significant mean difference, p<0.05)

CHAPTER 7

Discussion and conclusions

The results of the present analysis raise several important issues that need to be addressed: morphological differences within the hominoids, variation within the lorisids, similarities and differences in the wrist and ankle structures between the lorisids and hominoids, and, finally, the proconsulids in a comparative context. One of the most immediate observations noted in the course of this study is that there is huge variability within the hominoid group in their features of the wrist and ankle. This is most notable where elements of the *Pongo* ankle show considerable structural deviation from the pattern found in the other hominoids. Additionally, although *Hylobates* shows similarities to the African apes in many of the characters examined, differences are often apparent in the degree of the expression of certain features. The latter is evident among the lorisid genera also, which differ greatly in the degree of many characters despite superficial uniformity. Consequently, as any analysis based upon the premise that the hominoids are a uniform and cohesive group in terms of the characteristics in question would be fundamentally flawed, this analysis separates superfamily Hominoidea into smaller divisions for the purpose of examination.

HOMINOID CHARACTERISTICS

This analysis shows that Hominoidea can generally be divided into three main groups in the structure of their wrists and ankles: the African apes, *Pongo* and the hylobatids. These divisions are also apparent in the locomotor repertoires of the hominoids (knuckle-walking, quadrumanous climbing and bridging, and bimanual suspension, respectively), and these differences may reflect contrasting morphological adaptations to the variation in locomotor activities. Although the above is true for the overall construction of these two joints, certain individual features, however, are remarkably uniform within the hominoid group.

	African apes	*Pongo*	Hylobatidae	Cercopithecidae	Atelidae	Cebidae	Lemuridae	Lorisidae	Proconsulidae
IUSPL	short	short	moderately short	moderately short	moderately short	moderately long	moderately long	long	-
IUSPL2	short	short	moderately short	moderately short	moderately short	moderately long	moderately long	long	moderately short
IUCA	restricted	restricted	moderately restricted	Moderately extended	Moderately extended	extensive	extensive	Restricted – moderately restricted	-
IUHS	Almost square	Almost square	Slightly narrower mediolaterally	Considerably narrower mediolaterally	Considerably narrower mediolaterally	Considerably narrower mediolaterally	Slightly narrower mediolaterally	Slightly – considerably narrower mediolaterally	Slightly – considerably narrower mediolaterally
IRUA	Very extended	Very extended	extended	moderate	short	short	short	Moderately extended	-
IRUAFS	ML long	ML long	ML long	ML moderate	ML short - moderate	ML moderate	ML very short	ML moderate to long	-

Table 23: Summary of wrist indices across the genera studied

	African apes	*Pongo*	Hylobatidae	Cercopithecidae	Atelidae	Cebidae	Lemuridae	Lorisidae	Proconsulidae
ITD	shallow	Moderately shallow	shallow	Moderately deep	shallow	shallow	Moderately deep	deep	Moderately shallow to moderately deep
IAPTW1	Very wedged	Not very wedged	Very wedged	Moderately wedged	Very wedged	Moderately wedged	Almost parallel	Almost parallel, sometimes wedged other way	Very wedged
IAPTW2	Very wedged	Not very wedged	Very wedged	Moderately wedged	Very wedged	Not very wedged	Almost parallel	Almost parallel	Very wedged
IPCFD	Moderately deep	moderate	moderate	Very deep	shallow	moderate	Very deep	Very shallow	Moderately shallow – moderately deep
ASTA-LC	Very oblique 64/66	69	70	67/68	72/78	75	71	Varied 62/68/73/76	62/64/65

Table 24: Summary of talocrural and subtalar indices and angles across the genera studied

	African apes	*Pongo*	Hylobatidae	Cercopithecidae	Atelidae	Cebidae	Lemuridae	Lorisidae	Proconsulidae
ITHB1	Very broad	Very narrow	Moderately broad	Very narrow	Very narrow	Moderately narrow	Moderately broad	Moderately to very broad	Moderately narrow to moderately broad
ITHB2	Very flat	Fairly flat	Moderately rounded	Very rounded	Moderately rounded	Very rounded	Moderately rounded	Very flat	Moderately rounded
ITHNL	Very short	Moderately short	Moderate	moderate	long	long	moderate	Very short - moderate	Very long
ATH-LC	Very oblique	Moderately oblique	Moderately oblique	Less oblique	Moderately oblique	Moderately oblique	Moderately oblique	Moderately – very oblique	Moderately – less oblique (except dend very oblique)

Table 25: Summary of talar head and neck indices and angles across the genra studied

Pan and *Gorilla* are similar in most of the indices, either exclusively or within hominoids generally. This is expected, due to fundamental similarities in the locomotor repertoires of these genera. The only index where the African apes differ from one another is the index of anterioposterior talar wedging derived from the trochlea maximum and minimum breadths relative to the trochlea length. In this measurement, *Gorilla* shows comparatively extreme wedging, whilst *Pan* is intermediate between the cercopithecids and the atelids. Due to the overall similarities between the locomotor patterns of *Gorilla* and *Pan*, it is difficult to imagine the functional significance for this difference, as the talus in both genera is subject to the same kind of stresses, unless it can be attributed to body size differences for this particular mode of locomotion, or perhaps to increased terrestrialism in *Gorilla*. The *Gorilla* talar trochlea is relatively very short and broad. This apparently extreme morphology probably provides a robust structure for the transmission of the considerable forces incurred at this point by the gorilla's huge body weight during quadrupedal postures. The large surface area of the trochlea would also be adaptive for the relatively unpredictable direction of forces during limited arboreal activity, and a solid support during terrestrial activity. It is probably the extreme reduction in length of the *Gorilla* trochlea that contributes to the difference within the African apes.

Pongo, whilst fundamentally very similar to the African apes in its wrist morphology, differs from them in several indices pertaining to the shape of the talus and the orientation of its parts. The talar trochlea is relatively deeper in *Pongo* than in the other hominoids, and deeper than in the platyrrhine genera, as well; it is most comparable to that of *Varecia*. Additionally, in the two indices of trochlea wedging, *Pongo* differs from all of the other hominoids, showing mean values intermediate between the strepsirhines and monkeys in both. These results agree with those of Langdon (1986) but are surprising, as the depth and shape of the trochlea would effectively regulate mediolateral rotation, and thus flexibility, at the talocrural joint. *Pongo* habitually uses hindlimb assisted suspensory postures and locomotion, and it is reasonable to assume that this would require a large amount of flexibility at this joint, as the foot extends to grasp irregular substrates from an infinite number of positions. It must be noted, however, that *Varecia*, *Chiropotes* and *Alouatta* are also known to utilise hindlimb suspensory

positional behaviour (Tattersall, 1982; Meldrum et al., 1997; Meldrum, 1998; Fleagle, 1999), so within this context *Pongo* does not seem such an anomaly. It might be the case that increased flexibility of the hindlimb in these genera is maintained through different mechanisms. Langdon (1986) suggests that the congruency of the talocrural joint is largely irrelevant in traction, as it would have minimal affect on mobility, whilst in supportive posture it would be essential for stability. This is perhaps a reflection of the frequent suspensory and reaching function of the hindlimb in *Pongo*.

In the angle of the subtalar axis to the lateral crest, both *Pongo* and *Hylobates* show higher mean and maximum values than the African apes and the cercopithecoids. The Old World genera are, however, quite spread out in this index, with very large overlapping ranges, and thus show no particular patterning that might have implications for locomotor function, although the means for the African apes are slightly lower than those of the cercopithecids. The main difference, as also noted by Langdon (1986), lies between the Old and New World taxa, with the former showing more obliquity at this point, and thus greater accessory motion, and the latter having a remodelled subtalar articulation with the subtalar axis more perpendicular to the longitudinal axis of the foot.

Pongo is also quite different from the other hominoids in the first index of talar head breadth (derived from the mediolateral head breadth relative to trochlear breadth), and moderately different in the index of talar head and neck length (in relation to overall talus length). This study, therefore, concurs with Langdon's (1986), where he suggests that talar head breadth is different in *Pongo*, convergent with the atelids, but would disagree that similar convergence is apparent in talar head and neck elongation. This latter characteristic is found to be considerably shorter in *Pongo* than in any of the extant monkeys, despite elongation compared to the African apes. The short, robust African ape talar head and neck is probably related to the stresses incurred at this point, as a reflection of the magnitude and unpredictability of these forces. The more gracile nature of the *Pongo* and atelid talonavicular articulation, and the moderately elongated talar head and neck in *Pongo*, almost certainly reflects the reduced stresses sustained during inverted

postures, and may contribute to increased excursion of the joint in these positions (Langdon, 1986).

The final index in which *Pongo* differs from the African apes is that of the angle of the talar head to the lateral crest. *Pongo*, and to a lesser extent *Hylobates*, shows a comparatively lower angle than those of the African apes. This angle is related to the primary direction of forces during postural behaviour, and has also been associated with the extent of hallucal grasping (Langdon, 1986). A more medially orientated talar head and neck is generally seen in genera that utilise powerful hindlimb grasping. Despite the important hindlimb grasping component in its postural repertoire, *Pongo* has a reduced hallux in comparison to the other hominoids, which is probably less fundamental during postural behaviour (Fleagle, 1999). It is maybe for this reason that the talar head exhibits less medial torsion, and is more in line with the longitudinal axis of the foot. *Hylobates*, on the other hand, has a long muscular hallux (Fleagle, 1999) and thus the reasons for the moderate talar head torsion are not as evident. It could be inferred, however, that *Hylobates* does not incorporate a significant amount of powerful hindlimb grasping in its positional repertoire.

The apparent uniformity of the great ape wrist suggests underlying functional parallels, which would essentially negate a knuckle-walking hypothesis for the evolution of these features. Conversely, it is clear that the African apes and *Pongo* differ considerably in the structures of their tali, and this is probably related to the fundamental contrasts in the function of the foot. Evidently, the talus of the African apes is an essential weight-bearing structure, whilst maintaining a high degree of flexibility at this point. Conversely, the *Pongo* foot, like the atelids, fulfils a more suspensory function, maintaining mobility during traction and becoming more stable in upright postures. Consequently, the talus incurs minimum stresses during inverted postures, and stability during quadrupedal behaviour reduces the need for a robust structure, as forces become more predictably orientated.

The hylobatids are dissimilar to the other hominoids in several characters (in addition to those aforementioned), and are often found to be intermediate between

the monkey- and ape-like character states. In these cases, hylobatids show different affinities with the two groups across the range of characters. The indices in which the hylobatids differ most evidently from the great apes relate to the shape of the ulna styloid process, its carpal facet, the shape of the ulna head, and elements of the talar head and neck.

In both indices of ulna styloid process length, *Hylobates* grouped with the other hominoids in the table of mean values, but shows a value that is more similar to the New and Old World monkeys than the great apes. Indeed, the great apes all show extremely low values for this index (< 2.5) whilst the closest affinity for *Hylobates* is found with *Alouatta* and to a slightly lesser extent, the two cercopithecid genera. This is illustrated in the multiple comparison test, where the great apes are evidently dissimilar from all other groups, but the mean value for Hylobatidae is no different to those of the Atelidae and Cercopithecidae at the 95% confidence level. This relatively intermediate nature of the hylobatid ulna styloid process agrees with Lewis (1971a, 1972a-b, 1974), as does the observation that the articular surface for the hylobatid carpus is more distally and dorsally orientated, compared to the cercopithecid articulation orientated more towards the interior of the joint.

In the index of ulnocarpal articulation *Hylobates* is intermediate between the New and Old World monkeys and the hominoids, showing a mean value closer to that of the monkeys, and consistent with some of the lorisid genera. This, again, was highlighted by Lewis (1971a, 1972a-b, 1974) in his observations that the *Hylobates* wrist was very 'monkey-like' in its configuration retaining considerable ulnocarpal contact through a meniscus, but showing a change in shape of the ulna styloid process. It must be noted, however, that the *Hylobates* wrist is unique among primates in the presence of an extra bony ossicle, the os Daubentonii.

In the index of ulna head shape, the hylobatids are again grouped with the other hominoids (and *Varecia*), intermediate between the great apes and lorises, but show more similarity to the lorisids, in terms of mean values. In this instance, however, the lorises and hominoids are quite different to the monkey genera.

In the second measure of talar head breadth (comparison of mediolateral breadth against craniocaudal depth), *Hylobates* is again grouped with the great apes, but shows mean values closer to those of *Varecia* and *Alouatta*, and to a lesser extent *Cercopithecus*. This is again illustrated in the multiple comparisons test, where, although the hylobatids show no significant difference to the great apes, they also show no significant mean difference to the atelids and lemurids.

In the index of talar head and neck length, both *Pongo* and *Hylobates* fall within the lorisid range, rather than that of the African apes, and differ quite evidently from the latter in this feature, despite an apparent grouping of hominoids and lorisids in this character. The multiple comparison test results clearly show the variability within the hominoids, finding no significant difference between the hylobatids, *Pongo*, lorisids and *Varecia* at the 95% confidence level, but showing the African apes to be significantly different to the other taxa at the lower extreme of the range.

Overall, the differences between the hylobatids and African apes are not as blatant as those seen in *Pongo*, and can be best described as differences in degree of characters rather than structural variation. The findings of this study, in this respect, wholeheartedly support the view proposed by previous analyses that the Hylobatidae represent a somewhat intermediate phase of adaptation between the cercopithecids and African apes: a moderately reduced ulna styloid process and ulnocarpal articulation, reorganisation of the articular facets for the carpus and radius, low talar trochlea wedging but shallow trough, and reorganisation of the talar head and neck (Lewis, 1971a, 1972a, 1972b, 1974; Conroy and Fleagle, 1972; Langdon, 1986).

In several indices, mostly of the distal ulna but with one measure of talar head breadth, either the great apes, or all of the hominoids, are grouped together, although some of these groupings may be fairly loosely defined due the more intermediate character states of the hylobatids between the great apes and the other genera (as discussed above). Most particularly, the hominoids are quite uniform in ulna styloid process length, radial facet shape and talar head breadth

relative to craniocaudal height, and the great apes are closely grouped in the extent of ulnocarpal articulation and ulna head shape. These indices, which may indicate shared derived hominoid/great ape morphologies, could be the best sample for comparison with other taxa to look for patterns of convergence or homoplasy.

LORISOID CHARACTERISTICS

Although all lorises are similar in the morphological structures of their wrists and ankles, they show a certain amount of variation in the extent of characters among the four genera in some of the indices analysed. In the first index of ulna styloid process length the four loris genera form a clear group, unique compared to all other taxa in their comparatively long styloid process. *Arctocebus*, and to a lesser extent *Loris*, however, are far more extreme in this index than the other genera. It might be the case that the few samples used for these two genera are not representative of the taxa, but the specimens used for *Arctocebus* are uniformly high, falling either at the upper limit, or outside the range, of the other genera. In the second index of ulna styloid process length, however, it is *Loris* that seems to be more extreme, with *Arctocebus* to a lesser extent. The different results achieved for the two indices would suggest that variation is evident in the characters used as denominators for the indices, but the uniformly high indices for both genera in the two measures of ulna styloid process length do seem to confirm that *Arctocebus* and *Loris* are generally more extreme in this characteristic.

Similarly, *Arctocebus* seems to be rather different to the other taxa in the index of ulnocarpal articulation. This is more immediately evident as the other lorisids form a group within the hominoid range, whilst *Arctocebus* is more monkey-like in its larger ulnocarpal articulation. This enlarged articulation might be correlated with the fact that the styloid process is elongated in this genus, but this does not seem an adequate explanation in view of the fact that all the other lorises have comparatively long styloid processes, but reduced carpal facets. Cartmill and Milton (1977) note that the different lorisids show varying degrees of withdrawal of the ulna from the carpus both between and within genera, but they do not

include *Arctocebus*, they note, however, that *Perodicticus* is more advanced in this characteristic, and their *Nycticebus* sample included a specimen where the ulna was completely withdrawn from the primitive carpal articulation. As these two genera show the lowest indices for both ulna styloid process length and ulnocarpal articulation, it may therefore be inferred that the lower values for these characteristics may represent retraction of the ulna from direct participation in this joint. This does not, however, explain the relatively extreme nature of ulna styloid process length in a wider comparative context.

In the index of radioulnar articular facet shape, it is *Perodicticus* that appears to be different to the other lorises. It exhibits a relatively low mean value, intermediate between *Cercopithecus* and *Saimiri*, suggesting a mediolaterally short radial facet on the ulna. The remaining loris genera, whilst clearly grouped together, show affinities in their mean values to the hominoids. The mean values for *Arctocebus* and *Loris* within this group are again considerably higher than *Nycticebus*.

The results for characters of the wrist are very illuminating. Despite apparent grouping of the four genera among the lorisids, *Loris* and *Arctocebus* tend to differ from the others in the extent of expression of certain features. What is unusual, however, is the combination of features observed in these two genera: a relatively longer ulna styloid process, with a larger ulnocarpal articulation than seen in the other genera, and yet a mediolaterally longer radial facet on the ulna. These results are somewhat contradictory, in that the first two features may be seen as limiting for ulna deviation, whilst the third is representative of greater excursion of the radius around the ulna. Cartmill and Milton (1977) noted that *Loris* is slightly less advanced in characters of the ulnocarpal joint than *Perodicticus*. They maintain that the *Loris* ulna styloid process retains a small, distally placed articular facet, which only articulates directly with the carpus during dorsiflexion and ulna deviation. The authors suggest that this contact does not affect the degree of ulna deviation possible at the wrist. Unfortunately, their examination did not include the dissection of an *Arctocebus* specimen, but it is reasonable to assume that the same conclusions can be applied to this genus.

At the talocrural joint, the lorises are again grouped together for the depth of trochlea and the wedging indices, at the higher end of the primate range. Once again, however, *Loris* is the most extreme in all of these measures, with a comparatively deep trochlea and the lowest indices of wedging. This suggests that *Loris* possesses the most rigid talocrural joint, with a hinge-like movement restricted to the sagittal plane. It is clear that all of the lorisids are very different to the hominoids in the suite of features pertaining to this joint. In fact, lorisids are characterised by very limited mobility at the talocrural joint (Grand, 1967).

In the angle of the subtalar axis to the longitudinal axis of the foot, the lorisids are very spread out in their mean values. *Perodicticus* and *Arctocebus* are similar to the New World primates, both exhibiting very high mean values, whilst at the opposite extreme, the mean angle for the subtalar axis of *Nycticebus* is the lowest among extant primates, most similar to *Pan* and *Gorilla*. *Loris* is relatively intermediate in this angle, like the cercopithecids. The main division in the orientation of this angle is between the New and Old World primates, with convergence on the platyrrhine condition found in isolated Old World genera (i.e., *Pongo*; Langdon, 1986). New World taxa have a more perpendicular subtalar axis, compared to the more oblique axis found in the other genera, and these features are functionally related (Langdon, 1986; Strasser, 1988). It is interesting, therefore, to note such differences between the lorisids, although the huge ranges for all of the taxa studied suggests that a large amount of variability exists in all genera, and thus the New and Old World differences may not be quite so clear cut.

The lorisids, although uniformly high in both indices of talar head breadth, also exhibit a degree of variability in these measures. The ranges for each genus are, however, considerable in both indices, which makes it difficult to uncover any clear morphological patterns. All of the genera are grouped with the hominoids (except *Pongo* in the first index). This suggests, in accordance with both the observational data and previous studies (Grand, 1967), that the lorisids have relatively broad, flat talar heads.

COMPARISON BETWEEN THE HOMINOIDS AND LORISIDS

Across the range of characters examined, hominoids and lorisids (or divisions of them, in the case of the hominoids) either exhibit remarkably similar, or absolutely different morphology. What is apparent, however, is that the lorisids are very different from *Varecia* in many of the features considered. Additionally, the features in which an apparent convergence has taken place between the lorisid and hominoid genera are spread across both the wrist and ankle joints, and thus in both structures a combination of characteristics is observed in the lorisid genera.

In the two indices of ulna styloid process length the lorisids are at the opposite extreme from the hominoid group, and most particularly the great apes, in their considerable elongation of this structure. Indeed, the lorisid styloid process is shown to be markedly longer than any other taxa, whilst the hominoids exhibit the shortest relative lengths. Conversely, in the index of ulnocarpal articulation, the genera from both of these groups (with the exception of *Arctocebus*) show remarkable convergence, with the lorisids exhibiting greater reduction of this facet than any non-hominoid genus. Observations suggest, however, that the orientation of this facet is more consistent with a monkey-like pattern, distally placed but verging towards the interior of the joint. It is somewhat difficult to reconcile these results, as it might be expected that ulnar withdrawal from the carpus would be contingent on ulna styloid process reduction. It must be noted, however, that size, positioning and orientation of the carpus (most particularly the triquetral and pisiform) may have a fundamental bearing on the overall mobility of this joint.

In the index of ulna head shape, the lorisids (and *Varecia*) again show similarities to the hominoids, being intermediate between the great apes and monkeys in this aspect, and comparable with *Hylobates*. This suggests that these genera exhibit a less mediolaterally narrow ulna head, compatible with an extended radioulnar contact, as suggested by Harrison (1982). This is reiterated by the two measures of the radioulnar articulation, which suggests that the ulna side of this contact is both comparably large and extended mediolaterally. Both of these indices, whilst not different from cercopithecids at the 95% confidence level, show similarity to the character state of the hominoids. It might be inferred from these results that

the lorisids exhibit significant radial excursion around the ulna, which would contribute to overall mobility at the ulnocarpal joint (Cartmill and Milton, 1977).

Overall, therefore, the lorisid wrist joint shows a mosaic of characteristics at the ulnocarpal joint, with evident similarity to the hominoids in certain features. As Cartmill and Milton (1977) have suggested, the ulnocarpal contact is greatly reduced, and elements of the radioulnar articulation suggest a considerable degree of ulnar deviation. These features are, however, found in combination with an extraordinarily long and slender ulna styloid process, and an interiorly orientated ulnocarpal facet. The significance of ulna styloid process reduction has been emphasised in the many studies of the derived hominoid wrist as contributing to overall mobility (Lewis, 1971a, 1972a-b, 1974; O'Connor, 1975) and it seems that the lorisids have achieved similar movement capabilities, albeit perhaps to different degrees, without necessitating the diminution of this feature. As previously stated, it is difficult to achieve a good overall picture of the joint from isolated elements, and a more comprehensive study would need to take into account the structure and orientation of the carpus. Additionally, it would be beneficial to study the overall congruency of the articulated joint by dissection or radiograph to achieve a better understanding of how the elements interact as a whole.

In the indices pertaining to ankle mobility, the lorisids show different degrees of likeness to hominoids across the various joints, with the most evident similarities in the shape and orientation of the talar head and neck. At the talocrural joint, in the index of talar trochlea depth and both indices of trochlear wedging, the lorisids are uniformly opposite in extreme to the African apes and *Hylobates*. They do, however, show close affinities to *Pongo* in the wedging indices. These three indices can be directly related to the congruency, and consequently the degree of accessory movement, at this joint. The primate talar trochlea is secured between the mortise-like structure formed by the tibial and fibular malleolar facets, which effectively limits the range of motion at this joint to plantar/dorsiflexion. In the lorisids, where the trochlea has a relatively deep trough and is anteroposteriorly parallel sided, the mortise retains its secure hold throughout the range of motion, and movement is limited to a single plane. On the other hand, the African apes

and hylobatids show significant wedging, and a relatively shallowly curved trochlea trough, which would permit a greater degree of mediolateral rotation at the talocrural joint, particularly in dorsiflexed postures. The results of this study therefore suggest that the lorisids are different from these hominoids at the talocrural joint, and that the lorisid joint is fundamentally a hinge-like mechanism, with movement restricted to the sagittal plane (Grand, 1967).

At the subtalar joint, in the index of posterior calcaneal facet depth, the lorisids again show marked differences to the African apes, but slightly closer similarity to *Pongo* and *Hylobates*. With the atelids, the lorisids exhibit the lowest mean values for this index, representing a relatively shallow posterior calcaneal facet, and these two groups show no mean difference to one another at 95% confidence. The hominoids, in contrast, are more intermediate in this aspect, with the African apes verging towards the more extreme condition seen in cercopithecids, and the Asian apes showing closer affinities with the lorisids. The depth of curvature of this facet is important in that it dictates the range of excursion in inversion/eversion. A shallow facet facilitates a greater potential for these movements, whilst a deeply curved facet is more restrictive, as the opposite facet on the calcaneus is held more rigidly. Thus, the results of this study support a view that both the lorises and atelids have greater potential excursion than the hominoids at the subtalar joint, although hominoids exhibit more mobility than the cercopithecids (Langdon, 1986; Strasser, 1988). Grand (1967) noted the range of inversion/eversion in lorisids to be approximately 60-70°, which would be crucial in accommodation to inclined supports for these slow moving primates. *Varecia*, in this aspect, show morphology more consistent with that of the cercopithecids.

In features of the talar head and neck, the lorisids and African apes show remarkable similarity. In indices of talar head breadth, the results suggest that the lorisids, African apes and *Hylobates* all have mediolaterally broad and craniocaudally flattened talar heads, which indicates that the talonavicular articulations in these taxa are extensive, facilitating a wide range of mediolateral excursion at this point. The relative breadths of the talar head in these taxa also suggest that the radius of curvature is high, contributing to a fairly loose fitting

joint overall, and thus increased accessory mobility (Langdon, 1986). In talar head breadth, *Pongo* is more convergent with the atelids, as discussed above.

The talar head and neck in the hominoids and lorisids is also relatively short and more medially orientated (with the exception of *Pongo*) in comparison to the other primates. The short relative length and robusticity of these structures suggests that they are adapted to withstanding a significant degree of stress during everyday activities. The medial orientation indicates the primary direction of these stresses, perhaps as a response to enhanced grasping capabilities in the hallux (Langdon, 1986).

Overall, the ankle joints of the African apes, hylobatids and lorisids appear adapted to increased mobility, albeit with variable movement capabilities at the three articulations examined in this study. Hominoids have a large range of accessory motion at the talocrural joint, with moderate stability at the subtalar articulation, whilst lorisids have a particularly rigid talocrural joint, but increased subtalar mobility. The inferred orientation and degree of stress incurred at the talonavicular articulation appear remarkably similar in these taxa, which would suggest functional similarities at this point.

PROCONSULIDS IN A COMPARATIVE CONTEXT

Due to the limited fossil material it is impossible to attain a full data set for the proconsulid wrist indices; those included are derived from single specimens. Additionally, the specimen used for *Proconsul heseloni* (KNM-RU 2036) is a juvenile, and the results for this species must therefore be treated with further caution. Conversely, numerous tali from this period are preserved in good condition. Thus, comparable talar measurements were available across the range of indices, and for a variety of taxa.

The only wrist indices for which a meaningful analysis could be conducted between the fossil and extant genera are the second index of ulna styloid process length and the index of ulna head shape. In the former, single specimens from

Kalepithecus and *Proconsul* are available. Both genera show indices that fall between the mean values for *Hylobates* and the monkey genera, and well within the ranges of *Hylobates*, *Macaca*, *Alouatta* and *Cercopithecus*. In view of the intermediate nature of the *Hylobates* distal ulna, this suggests a broadly monkey-like ulna styloid process (Morbeck, 1975; Harrison, 1982, 1987). On the basis of these results, the suggestion that the proconsulid ulna styloid process is more advanced than *Hylobates* (Lewis, 1971a, 1972a, 1972b, 1974) is falsified. Again, analysis on the basis of single specimens and isolated elements is at best speculative, and it may be, as seen with the lorisid wrist joint, that this particular index may not be as fundamental in determining locomotor capabilities as has previously been thought. Indications from previous studies suggest that the proconsulid carpus and ulnocarpal articulations exhibit significant reorganisation towards a more great-ape-like morphology (Lewis 1971a; Beard et al., 1986) and this cannot be discounted by the current analysis. A combination of long styloid process, reorganised carpus and reduced ulnocarpal facet is, after all, characteristic of the lorisids who exhibit significant ulnar deviation (Cartmill and Milton, 1977).

In the index of ulna head shape, the single *Kalepithecus* specimen has a shape comparable to the Old and New World monkeys (mediolaterally narrow), whilst the *Proconsul* individual is within the range of means exhibited by the lorisids (slightly broader mediolaterally). Both fossils, however, fall within the ranges found in all of the extant genera except the great apes, and thus neither can be considered to be particularly ape-like in this index. A mediolaterally broader ulna head suggests an extended radial facet, and thus the greater excursion of the radius around the ulna characteristic of ulna deviation. This is not overwhelmingly apparent in the fossil taxa, despite the relatively high index in *Proconsul*.

It is difficult to come to any concrete conclusions about the wrist morphology of these Miocene genera from the limited data set derived from isolated specimens. Overall, these fossils do not show any obvious similarities to the derived hominoid morphology, and inference can only be tentative without a more detailed analysis of the specimens in question and other elements of the wrist.

Even so, a much richer fossil record in this aspect of postcrania would be necessary before any more concrete assertions could be made.

For the talar indices, measurements of fossils were available for *Proconsul* (10), *Dendropithecus* (2), *Rangwapithecus* (3), *Kalepithecus* (3) and *Limnopithecus* (2), although data sets were not complete for all specimens due to variable preservation. With relation to the talocrural joint, the proconsulids show moderate talar trochlea depth, with means intermediate between those of the New World genera and *Pongo*; the exception is *Kalepithecus*, which is more consistent with the cercopithecids. The multiple comparison test shows that the proconsulids differ significantly ($p<0.05$) from the hylobatids and African apes in this index. In both indices of trochlear wedging, however, all of the fossils show values within, or above, the mean range for the African apes and *Hylobates*. In both of the wedging indices, the mean values for the fossil taxa are no different to those of the atelids, hylobatids and African apes at the 95% confidence level. At this level, however, they differ significantly from the cercopithecids.

These results are somewhat at odds with previous studies, which have suggested that the proconsulids exhibit limited wedging and relatively deep talar trochleas (Harrison, 1982; Langdon, 1986). It is recognised, however, that these earlier analyses were limited to an evaluation of the proconsulids in a comparative context with cercopithecids and hominoids, and this study has found that it is actually the lorisids that show the extreme trochlear depth and most limited wedging. Cercopithecids in this study, however, are more intermediate in these characters, rather than at the opposite extreme to the hominoids. Nevertheless, the wedging index results are certainly different enough from those of earlier studies to warrant further investigation. If these results are shown to be accurate, it suggests that the range of accessory motion at this joint in the fossil genera is equivalent to the hominoids across the range of dorsi/plantarflexion. The relatively moderate depth of the talar trochlea also suggests a degree of mobility at this joint, although this is somewhat equivocal.

In the index of posterior calcaneal facet depth, the fossils are relatively spread out across the extant primate range of means, but the specimens for *Limnopithecus*,

Rangwapithecus and *Dendropithecus* visibly fall towards the lower end of the range, most comparable with the lorisids and atelids. The means for these genera all fall outside the range of variation seen in the cercopithecids. *Proconsul* and *Kalepithecus*, however, are most similar to the African apes, and have upper range limits that overlap those of the cercopithecids, but are below their mean values. The subtalar axes of all of the fossils are consistent with an Old World pattern of significant obliquity.

These results indicate that the subtalar joint, in at least some of the fossil taxa, is considerably more mobile than the Old World monkey genera, and perhaps more mobile than the African apes, converging towards the apparent extreme mobility seen in the lorisids and atelids. This is evident in the multiple comparison test, where the cercopithecids seem unique in their extreme depth of curvature of this feature, whilst the proconsulids show no significant mean difference to the hominoids, and with *Pongo* are verging towards the lorisid and atelid character state in this feature. These results are similar to those found by Langdon (1986) in this aspect of proconsulid morphology, but they are contrary to those reported by Harrison (1982), who suggests that the subtalar morphology of the fossil taxa is most reflective of generalised arboreal quadrupedalism.

In the indices of talar head breadth, the proconsulids are somewhat intermediate between the means of the monkeys and the African ape/hylobatid/lorisid grouping. In the first index, the means for the extant taxa fall into two distinct groupings: the Old and New World monkeys and *Pongo* all have means below 113, whilst the other hominoids and the strepsirhines have mean values above 127 (although the ranges for each genus are fairly widespread). To a certain extent, the fossil taxa bridge the gap between these groups, although they are more similar to the monkeys at the 95% confidence level in the multiple comparison of means. In the second index of talar head shape, the proconsulids are most comparable to the monkeys and *Varecia*, exhibiting a more rounded talar head very different to that of the great apes and lorisids. This is evident in both the means and ranges of the taxa for which multiple specimens were examined, and the individual results. The highest fossil value is seen in *Limnopithecus*, which marginally exceeds the mean for *Hylobates*, but on the basis of a single specimen it is very difficult to make

sweeping statements about the extant affinities of a fossil genus. This is especially true since this value fall within the upper limits for *Cercopithecus*, *Varecia* and *Alouatta*.

In the index of talar head and neck length and angle of talar head torsion, the proconsulids are quite varied, with the genera examined showing widely different character states from one another. The *Proconsul* sample, derived from five specimens, is remarkably similar to the hominoid genera in the index of talar head and neck length, falling well within the apparent hominoid/lorisid grouping. The *Proconsul* range is also very similar to those seen in *Perodicticus* and *Nycticebus,* and almost comparable to *Hylobates*. Some specimens fall within the upper limits of the African ape ranges. In the angle of the talar head and neck from the lateral crest, however, *Proconsul* shows limited torsion, more consistent with that of the monkeys. These results would support a view that the *Proconsul* talar head and neck is short and robust, probably in accommodation to considerable stresses, but the angle of torsion suggests, however, that these stresses were more longitudinally orientated, rather than medially as seen the African apes.

Kalepithecus is at the other end of the primate range in talar head and neck length, with mean value most comparable to the ceboids, indicating a more elongated talar neck. The two individuals used to represent this genus, however, also fall within the upper limits of *Nycticebus*, *Perodicticus* and *Hylobates*, but not *Proconsul*. This suggests, therefore, that the two fossil genera are fundamentally different from one another in this characteristic. *Kalepithecus* also exhibits the lowest angle of talar head torsion across the whole extant and fossil range, and therefore the lowest mean. These results suggest that *Kalepithecus* is similar in aspects of talar neck shape and orientation to the atelids.

The single specimen for *Dendropithecus* is intermediate in the index of talar head and neck length, with a value that is within all of the non-African ape primate ranges. The talar head and neck, however, shows considerable medial orientation; comparable to *Gorilla*. This value is within the ranges seen in all of the hominoids, *Nycticebus* and *Perodicticus*. Thus, few reliable inferences can be made about the talar head and neck of this genus in its relation to the extant taxa,

although the angle of talar head torsion suggests certain similarities with the hominoid and lorisid genera.

Overall these results are in accord with those found by Langdon (1986); he suggested that the specimens now attributed to *Kalepithecus* show parallel features of the talar head and neck to the atelines, perhaps indicating a degree of suspensory locomotion within their repertoires. *Proconsul*, on the other hand, is characterised by a short head and neck, more similar to the extant hominoids. Langdon (1986: 173) is also cautious in his inferences about *Dendropithecus*, suggesting that the limited material could not warrant "behavioural conclusions".

Overall the proconsulid ankle represents a mosaic of features across the three talar joints examined here, and shows similarities to the cercopithecids, hominoids, and lorisids to different degrees in various features. At the talocrural joint, it seems that the early Miocene fossils have high anteroposterior wedging, which would suggest that this joint would allow a high degree of accessory mobility in dorsiflexed postures, most particularly inversion/eversion. On the other hand, the moderate depth of the trochlear trough suggests that the foot retains a reasonable degree of congruency, and probably more restricted mediolateral rotation than seen in African apes and *Hylobates*. This also suggests greater stability in plantarflexed positions.

The subtalar joint, in contrast, is more like that of the extant hominoids, and may well be considerably more mobile. The results for the depth of the posterior calcaneal facet show the fossil genera converging towards the lorisids and atelines in this feature, with movement capabilities at least equal to the hominoids, and considerably more mobile than the cercopithecids.

The talar breadths relative to the trochlea in these genera are somewhat intermediate between the monkey and African ape/*Hylobates*/lorisid grouping, but are much more rounded than seen in lorises and hominoids. The talar head and neck length is varied, with *Proconsul* showing close comparison to the African apes and *Hylobates*, despite reduced torsion, whilst *Kalepithecus* resembles atelids in both length and orientation of this structure.

EVALUATION

The findings described here do not falsify the hypothesis that the evolution of hominoid locomotion may have derived from a slow, deliberate arboreal quadruped. Elements of the wrist of the lorisids and hominoids show several similarities (reduction of the ulnocarpal contact, mediolateral expansion of the radial head and the radioulnar facet). Additionally, although these groups differ in characters previously thought suggestive of substantial contact between the ulna and the carpus (orientation of the carpal facet and length of the styloid process), the significance of these features in determining the relationship of this joint must be seriously questioned in the light of the combined results of the present analysis and that of Cartmill and Milton (1977). It is clear that the elongation of the styloid process has little bearing on joint congruency in the lorisids, and thus cannot be used as a reliable indicator in the analysis of fossil forms. The relative position of the proconsulids in this index, therefore, is virtually meaningless with this knowledge. It has been suggested, however, that the carpal anatomy of *Proconsul* shows some structural similarities to the extant hominoids (Beard et al., 1986) and, therefore, there is no reason to assume that the early Miocene taxa did not have a similar ulnocarpal joint to lorisids. It is possible that reduction of the styloid process was a response to its relative redundancy, although the contact maintained (albeit limited) between the shortened ulna styloid process and the carpus in *Pan* suggests that this is not the case. Full understanding of the relationship of the joint as a whole cannot be achieved without examination of the carpus, and analysis of the articulated joint.

In ulna head and radial facet shape, hominoids and lorisids show clear similarities, but the fossil material is again inconclusive. It is possible that these taxa may have shown equivalent ranges of ulna deviation to the lorises, and thus locomotor similarities, due to their results for the ulna head shape falling well within the ranges of these extant taxa. Again, this concurs with Odhiambo Nengo and Rae (1992) who suggest that the morphology of the *Proconsul major* ulna head resembles that of extant hominoids, but is contrary to Harrison (1982, 1987).

In the talus, again, elements show distinct similarity between the lorisids and hominoids; notably features of the talar head and neck. The two groups differed in the other joints, however, with the lorises showing more mobility in the subtalar joint, and the hominoids having greater accessory motion at the talocrural joint (Grand, 1967; Langdon, 1986). Proconsulids show similarities to the hominoids in certain features of the trochlea, and thus are quite different to the lorises, but at the subtalar joint most of the taxa were closer in their morphology to lorisids. The talar head and neck in most of the fossil taxa is intermediate between the monkeys and the African ape/*Hylobates*/lorisid grouping. Again these results do not falsify the hypothesis examined, as the fossil taxa appear to have some development of the shared lorisid and hominoid features, and similarities to either the hominoids or lorises across the range of other characters. What is evident, however, is that the proconsulids do seem to exhibit different character states to one another in some of the features, with *Kalepithecus*, like *Pongo*, converging on an ateline condition in features of the head and neck, in contrast to the more hominoid condition seen in the other specimens. This would certainly call into question the supposition that the early Miocene hominoids were relatively uniform in their postcrania, and thus adapted for similar locomotor behaviours (Rose, 1996). It is possible that these genera were, like many of the extant taxa, similar in their main locomotor pattern but combining this with differential use of supplementary behaviours.

Unfortunately, inference has to be relatively cautious on the basis of isolated postcranial parts (Sanders and Bodenbender, 1993). Additionally, this study has shown that all primates show a large range of variation for many of the characters studied; where a single individual represents a whole genus, it is very hard to establish exact relationships of the fossil taxa within an extant framework.

This study has raised some points for further research, particularly with reference to the postcranial similarities of the lorisids and hominoids. These taxa show similarities in features of both the ankle and wrist joints that relate to hand and foot orientation and increased mobility, and it would be worthwhile examining other parts of the postcrania of these groups to find out if these similarities can be

seen, and, again, compared with the early Miocene forms. In addition, further studies need to address the particular characters examined here in combination with the other components of the joints, perhaps also looking at the articulated joints through dissection or radiographs, to gain a more detailed picture of how the joints manoeuvre as a whole.

The biggest problem encountered in this and other studies is the limitations of the fossil material for particular postcranial parts, and the small sample sizes of some fossil genera. Unfortunately, whilst analyses can become more rigorous with the development of new techniques, the fossil record will always be fragmentary and thus, inference can only be tentative.

CONCLUSIONS

The hypothesis that hominoid locomotion evolved from a lorisid-like deliberate quadrupedalism was tested. Several features of the ankle and wrist morphology were measured in lorisids and hominoids, with a comparative group of other arboreal quadrupeds from across the order Primates. The measurements were converted into indices for the purpose of statistical analysis. These were further compared with previous data of the early Miocene hominoid genera.

The results suggest that the lorisids and hominoids share some features of their postcrania, although they are also remarkably different in others. Furthermore, the results indicate that the proconsulids share features with both the lorisids and hominoids, to different degrees in the various features. Although the results cannot conclusively confirm the ancestral locomotor pattern to be lorisid-like, they support a notion that shared characteristics are functionally related and thus a basal hominoid had movement capabilities in certain joints not dissimilar to extant lorisids.

References

Aiello, L.C. (1981) Locomotion in the Miocene Hominoidea. In C. Stringer (ed.) *Aspects of Human Evolution*, pp.63-98. Taylor and Francis: London.

Andrews, P. (1974) New species of *Dryopithecus* from Kenya. *Nature* 249: 188-190.

Andrews P. (1978) A revision of the Miocene Hominoidea of East Africa. *Bull. Br. Mus. Nat. Hist. (Geol.)* 30: 85-224.

Andrews, P., Begun, D.R. and Zylstra, M. (1997) Interrelationships between functional morphology and Paleoenvironments in Miocene hominoids. In D.R. Begun, C.V. Ward and M.D. Rose (eds.) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 29-58. Plenum Press: New York.

Andrews, P. and Groves, C.P. (1976) Gibbons and brachiators. In Rumbaugh, D.M. (ed.) *Gibbon and Siamang: A Series of Volumes on the Lesser Apes, vol. 4, Suspensory Behaviour, Locomotion, and Other Behaviours of Captive Gibbons; Cognition.* pp. 167-218.

Andrews, P and Simons, E. (1977) A new African Miocene gibbon-like genus, *Dendropithecus* (Hominoidea, Primates) with distinctive postcranial adaptations: its significance to origin of Hylobatidae. *Folia Primatol.* 28: 161-169.

Ankel-Simons, F. (1983) *A Survey of Living Primates and Their Anatomy.* Macmillan Publishing Co., Inc.: New York.

Ashton, E.H. and Oxnard, C.E. (1964) Locomotor patterns in primates. *Proc. Zool. Soc. Lond.* 142: 1-28.

Barnett, C.H. (1970) Talocalcaneal movements in mammals. *J. Zool.* 160: 1-7.

Beard, K.C., Teaford, M.F. and Walker, A. (1986) New wrist bones of *Proconsul africanus* and *Proconsul nyanzae* from Rusinga Island, Kenya. *Folia Primatol.* 47: 97-118.

Begun, D.R., Teaford, M.F. and Walker, A. (1994) Comparative and functional anatomy of *Proconsul* phalanges from the Kaswanga primate site, Rusinga Island, Kenya. *J. Hum. Evol.* 26: 89-165.

Bergeson, D.J. (1998) Patterns of suspensory feeding in *Alouatta pattiata*, *Ateles geoffroyi* and *Cebus capucinus*. In Strasser et al. (eds.) *Primate Locomotion: Recent Advances*, pp.45-60. Plenum Press, New York.

Cant, J.G.H. (1986) Locomotion and feeding postures of spider and howling monkeys: field studies and evolutionary interpretation. *Folia Primatol.* 46: 1-14.

Cant, J.G.H. (1988) Positional behaviour of long-tailed macaques (*Macaca fascicularis*) in Northern Sumatra. *Am. J. Phys. Anthropol.* 76: 29-37.

Cant, J.G.H, Youlatos, D. and Rose, M.D. (2001) Locomotor behaviour of *Lagothrix lagothricha* and *Ateles belzebuth* in Yasuni National Park, Ecuador: general patterns and non-suspensory modes. *J. Hum. Evol.* 41: 141-166.

Cartmill, M. and Milton, K. (1977) The lorisform wrist joint and the evolution of brachiating adaptations in the Hominoidea. *Am. J. Phys. Anthropol.* 47: 249-272.

Conroy and Fleagle (1972) Locomotor behaviour in living and fossil pongids. *Nature* 237: 103-104.

Conroy and Rose (1983) Evolution of the primate foot from the earliest primates to the Miocene hominoids. *Foot and Ankle* 3: 342-364.

Corruccini, R.S., Ciochon, R.L. and McHenry, H.M. (1976) The postcranium of Miocene hominoids: were dryopithecines merely 'dental apes'? *Primates* 17: 205-223.

Dagosto and Gebo (1998) Methodological issues in studying positional behaviour. In E. Strasser, J. Fleagle, A. Rosenberger and H. McHenry (eds.) *Primate Locomotion: Recent Advances*, pp. 5-29. Plenum Press: New York.

Day, M.H. (1979) The locomotor interpretation of fossil primate postcranial bones. In M.E. Morbeck, H. Preuschoft and N. Gomberg (eds.) *Environment, Behaviour, and Morphology: Dynamic Interactions in Primates*, pp. 245-258. Gustav Fisher: New York.

Day, M.H. and Wood, B.A. (1969) Hominoid tali from East Africa. *Nature* 222: 591-592.

Defler, T.R. (1999). Locomotion and posture in *Lagothrix lagotricha*. *Folia Primatol.* 70: 313-327.

Dykyj, D. (1980) Locomotion of the slow loris in a designed substrate context. *Am. J. Phys. Anthropol.* 52: 577-586.

Erikson, G.E. (1963). Brachiation in New World monkeys and anthropoid apes. *Symp. Zool. Soc. Lond.* 10: 135-163.

Feldesman, M.R. (1982) Morphometric analysis of the distal humerus of some Cenozoic catarrhines: the late divergence hypothesis revisited. *Am. J. Phys. Anthropol.* 59: 73-95.

Fleagle, J.G. (1976) Locomotion and posture of the Malayan Siamang and implications for human evolution. *Folia Primatol.* 26: 245-269.

Fleagle, J.G. (1980) Locomotion and posture. In D.V. Chivers (ed) *Malayan Forest Primates: Ten Years' Study in Tropical Rainforest*, pp. 191-207. Plenum Press: New York.

Fleagle, J.G. (1983) Locomotor adaptations of Oligocene and Miocene hominoids and their phyletic implications. R.L. Ciochon and R.S. Corruccini (eds.) *New Interpretations of Ape and Human Ancestry*, pp. 301-324. Plenum Press: New York.

Fleagle, J.G. (1986) The fossil record of early catarrhine evolution. In B. Wood, L. Martin and P. Andrews (eds.) *Major Topics in Primate and Human Evolution*, pp. 130-149. Cambridge University Press: Cambridge.

Fleagle, J.G. (1999) *Primate Adaptation and Evolution*. Academic Press: San Diego.

Fleagle, J.G. and Mittermeier, R.A. (1980). Locomotor behaviour, body size, and comparative ecology of seven Surinam monkeys. *Am. J. Phys. Anthropol.* 52: 301-314.

Fleagle, J.G. and Simons, E.L. (1978) *Micropithecus clarki*, a small ape from the Miocene of Uganda. *Am. J. Phys. Anthropol.* 49: 427-440.

Fleagle, J.G., Stern, J.T., Jungers, W.L., Susman, R.L., Vangor, A.K. and Wells, J.P. (1981) Climbing: a biomechanical link with brachiation and with bipedalism. *Symp. Zool. Soc. Lond.* 48: 359-375.

Ford, S.M. (1988) Postcranial adaptations of the earliest platyrrhine. *J. Hum. Evol.* 17: 155-192.

Gebo, D.L. (1992) Plantigrady and foot adaptation in African apes: implications for hominid origins. *Am. J. Phys. Anthropol.* 89: 29-58.

Gebo, D.L. (1996) Climbing, brachiation and terrestrial quadrupedalism: historical precursors of hominid bipedalism. *Am. J. Phys. Anthropol.* 101: 55-92.

Gebo, D.L., Beard, K.C., Teaford, M.F., Walker, A., Larson, S.G., Jungers, W.L. and Fleagle, J.G. (1988) A hominoid proximal humerus from the early Miocene of Rusinga Island, Kenya. *J. Hum. Evol.* 17: 393-401.

Gebo, D.L. and Chapman, C.A. (2000) Locomotor behaviour in Ugandan monkeys. In P.F. Whitehead and C.J. Jolly (eds.) *Old World Monkeys*, pp. 480-495. Cambridge University Press: Cambridge.

Gebo, D.L and Dagosto, M. (1988) Foot anatomy, climbing, and the origin of the Indriidae. *J. Hum. Evol.* 17: 135-154.

Gebo, D.L., MacLatchy, L., Kityo, R., Deino, A., Kingston, J. and Pilbeam, D. (1997) A hominoid genus from the early Miocene of Uganda. *Science* 276: 401-404.

Godfrey, L.R. (1988) Adaptive diversification of Malagasy strepsirhines. *J. Hum. Evol.* 17: 93-134.

Gomberg, D.N. (1985) Functional differences of three ligaments of the transverse tarsal joint in hominoids. *J. Hum. Evol.* 14: 553-562.

Grand, T.I. (1967) The functional anatomy of the ankle and foot of the slow loris (*Nycticebus coucang*). *Am. J. Phys. Anthropol.* 26: 207-218.

Grand, T.I. (1968) The functional anatomy of the lower limb of the Howler monkey (*Alouatta caraya*). *Am. J. Phys. Anthropol.* 28: 163-182.

Hamrick, M.W., Simons, E.L. and Jungers, W.L. (2000) New wrist bones of the Malagasy giant subfossil lemurs. *J. Hum. Evol.* 38: 635-650.

Harrison, T. (1982) *Small Bodied Apes from the Miocene of East Africa.* Ph.D. dissertation, University College London.

Harrison, T. (1987) The phylogenetic relationships of the early catarrhine primates: a review of the current evidence. *J. Hum. Evol.* 16: 41-80.

Harrison, T. (1988) A taxonomic revision of the small catarrhine primates from the early Miocene of East Africa. *Folia Primatol.* 50: 59-108.

Hopwood (1933) Miocene primates from Kenya. *J. Linn. Soc. (Zool.) Lond.* 38: 437-464.

Jenkins, F.A. (1981) Wrist rotation in primates: a critical adaptation for brachiators. *Symp. Zool. Soc. Lond.* 48: 429-451.

Jenkins and Fleagle (1975) Knuckle-walking and the functional anatomy of the wrists of living apes. In R.H. Tuttle (ed.) *Primate Functional Morphology and Evolution*, pp. 213-227. Mouton: The Hague.

Jungers, W.L. (1979) Locomotion, limb proportions, and skeletal allometry in emurs and lorises. *Folia Primatol.* 32: 8-28.

Jungers, W.L. (1979) Relative joint size and hominoid locomotor adaptations with implications for the evolution of hominid bipedalism. *J. Hum. Evol.* 17: 247-265.

Kay and Covert (1984) Anatomy and behaviour of extinct primates. In B. Wood, L. Martin and P. Andrews (eds.) *Major Topics in Primate and Human Evolution*, pp. 467-508. Cambridge University Press: Cambridge.

Kelley, J. (1997) Paleobiological and phylogenetic significance of the life history in Miocene hominoids. In D.R. Begun, C.V. Ward and M.D. Rose (eds.) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 173-208. Plenum Press: New York.

Kelley, J. and Pilbeam, D. (1986) The Dryopithecines: taxonomy, comparative anatomy, and phylogeny of Miocene large hominoids. In D.R. Swindler and J. Erwin (eds.) *Comparative Primate Biology, Volume 1: Systematics, Evolution and Anatomy*, pp. 361-411. Alan R. Liss, Inc.: New York.

Langdon, J.H. (1984) *A Comparative Functional Study of the Miocene Hominoid Foot Remains*. Ph.D. dissertation, Yale University, New Haven.

Langdon, J.H. (1985) Fossils and the origin of bipedalism. *J. Hum. Evol.* 14: 615-635.

Langdon, J.H. (1986) *Functional morphology of the Miocene hominoid foot: Contributions to Primatology, Vol. 22*. Karger: Basel.

Larson, S.G. (1996) Estimating humeral torsion on incomplete fossil anthropoid humeri. *J. Hum. Evol.* 31: 239-257.

Larson, S.G. (1998) Parallel evolution in the hominoid trunk and forelimb. *Evol. Anthropol.* 6(5): 87-99.

Le Gros Clark, W.E. (1952) Report on fossil hominoid material collected by the British-Kenya Miocene Expedition, 1949-1951. *Proc. Zool. Soc. Lond.* 122: 273-286.

Le Gros Clark, W.E. and Leakey, L.S.B. (1951) The Miocene Hominoidea of east Africa. *Fossil mammals of Africa No. 1*. British Museum (Natural History): London.

Leakey, M. and Walker, A. (1997) *Afropithecus*: function and phylogeny. In D.R. Begun, C.V. Ward and M.D. Rose (eds.) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 225-240. Plenum Press: New York.

Leakey, R.E. and Leakey, M.G. (1986a) A new Miocene hominoid from Kenya. *Nature* 324: 143-146.

Leakey, R.E. and Leakey, M.G. (1986b) A second new Miocene hominoid from Kenya. *Nature* 324: 146-148.

Leakey, R.E. and Leakey, M.G. (1987) A new Miocene small-bodied ape from Kenya. *J. Hum. Evol.* 16: 369-387.

Leakey, R., Leakey, M. and Walker, A. (1988a) Morphology of *Turkanapithecus kalakolensis* from Kenya. *Am. J. Phys. Anthropol.* 76: 277-288.

Leakey, R., Leakey, M. and Walker, A. (1988b) Morphology of *Afropithecus turkanensis* from Kenya. *Am. J. Phys. Anthropol.* 76: 289-307.

Lewis, O.J. (1971a) Brachiation and the early evolution of the Hominoidea. *Nature* 230: 577-579.

Lewis, O.J. (1971b) The contrasting morphology found in the wrist joint of semi-brachiating monkeys and brachiating apes. *Folia Primatol.* 16: 248-256.

Lewis, O.J. (1972a) Evolution of the hominoid wrist. In R. Tuttle (ed) *The Functional and Evolutionary Biology of Primates*, pp. 207-222. Aldine-Atherton: Chicago.

Lewis, O.J. (1972b) Osteological features characterizing the wrists of monkeys and apes, with a reconsideration of this region in *Dryopithecus (Proconsul) africanus*. *Am. J. Phys. Anthropol.* 36: 45-58.

Lewis, O.J. (1974) The wrist articulation of the Anthropoidea. In F. Jenkins (ed.) *Primate Locomotion*, pp. 143-169. Academic Press: New York.

Lewis, O.J. (1980a) The joints of the evolving foot, Part I: the ankle joint. *J. Anat.* 130: 527-543.

Lewis, O.J. (1980b) The joints of the evolving foot, Part II: the intrinsic joints. *J. Anat.* 130: 833-857.

Lewis, O.J. (1980c) The joints of the evolving foot, Part III: the fossil evidence. *J. Anat.* 131: 275-298.

Lewis, O.J. (1981) Functional morphology of the joints of the evolving foot. *Symp. Zool. Soc. Lond.* 46: 169-188.

Lewis, O.J., Hamshere, R.J. and Bucknill, T.M. (1970) The anatomy of the wrist joint. *J. Anat.* 106(3): 539-552.

Lisowski, F.P., Albrecht, G.H. and Oxnard, C.E. (1974) The form of the talus in some higher primates: a multivariate study. *Am. J. Phys. Anthropol.* 41:191-216.

Lisowski, F.P., Albrecht, G.H. and Oxnard, C.E. (1976) African fossil tali: further multivariate morphometric studies. *Am. J. Phys. Anthropol.* 45: 5-18.

McHenry, H.M and Corruccini, R.S. (1983) The wrist of *Proconsul africanus* and the origin of hominoid postcranial adaptations. In R.L. Ciochon and R.S. Corruccini (eds.) *New Interpretations of Ape and Human Ancestry,* pp. 353-368. Plenum Press: New York.

MacInnes, D. (1943) Notes on the East African Miocene primates. *J. East Af. And Ugan. Nat. Hist. Soc.* 18: 141-181.

MacLatchy, L. (1998) Reconstruction of hip joint function in extant and fossil primates. In E. Strasser, J. Fleagle, A. Rosenberger and H. McHenry (eds.) *Primate Locomotion: Recent Advances*, pp. 111-130. Plenum Press: New York.

MacLatchy, L.M. and Bossert, W.H. (1996) An analysis of the articular surface distribution of the femoral head and acetabulum in anthropoids, with implications for hip function in Miocene hominoids. *J. Hum. Evol.* 31: 425-453.

MacLatchy, L., Gebo, D., Kityo, R. and Pilbeam, D. (2000) Postcranial functional morphology of *Morotopithecus bishopi*, with implications for the evolution of modern ape locomotion. *J. Hum. Evol.* 39:159-183.

Meldrum, D.J. (1993) On plantigrady and quadrupedalism. *Am. J. Phys. Anthropol.* 91: 379-381

Meldrum, D.J. (1998) Tail-assisted hindlimb suspension as a transition in the evolution of the platyrrhine prehensile tail. In E. Strasser, J. Fleagle, A. Rosenberger and H. McHenry (eds.) *Primate Locomotion: Recent Advances*, pp. 145-156. Plenum Press: New York.

Meldrum, D.J., Dagasto, M. and White, J. (1997) Hindlimb suspension and hind foot reversal in *Varecia variegata* and other arboreal mammals. *Am. J. Phys. Anthropol.* 103: 85-102.

Mendel, F. (1976). Postural and locomotor behaviour of *Alouatta palliata* on various substrates. *Folia Primatol.* 26: 36-53.

Mittermeier, R.A. (1978). Locomotion and posture in *Ateles geoffroyi* and *Ateles paniscus*. *Folia Primatol.* 30: 161-193.

Mittermeier, R.A. and Fleagle, J.G. (1976). The locomotor and postural repertoires of *Ateles geoffroyi* and *Colobus guereza*, and a revaluation of the locomotor category semibrachiation. *Am. J. Phys. Anthropol.* 45: 235-256.

Morbeck, M.E. (1975) *Dryopithecus africanus* forelimb. *J. Hum. Evol.* 4: 39-46.

Morbeck, M.E. (1983) Miocene hominoid discoveries from Rudabanya: implications from the postcranial skeleton. In R.L. Ciochon and R.S. Corruccini

(eds.) *New Interpretations of Ape and Human Ancestry*, pp. 369-404. Plenum Press: New York.

Napier, J. (1963) Brachiation and brachiators. *Symp. Zool. Soc. Lond.* 10: 183-195.

Napier, J.R. and Davis, P.R. (1959) The forelimb skeleton and associated remains of *Proconsul africanus. Fossil Mammals of Africa No. 16.* British Museum (Natural History): London.

Napier, J.R. and Napier, P.H. (1967). *A Handbook of Living Primates.* Academic Press: London.

Napier, J.R. and Walker, A.C. (1987) vertical clinging and leaping: a newly recognised category of locomotor behaviour of primates. In R.L. Ciochon and J.G. Fleagle (eds.) *Primate Evolution and Human Origins*, pp. 64-68. Aldine de Gruyter: New York.

O'Connor, B.L. (1975) The functional morphology of the cercopithecoid wrist and inferior radioulnar joints, and their bearing on some problems in the evolution of the Hominoidea. *Am. J. Phys. Anthropol.* 43: 113-122.

O'Connor, B.L. and Rarey, K.E. (1979) Normal amplitudes of radioulnar pronation and supination in several genera of anthropoid primates. *Am. J. Phys. Anthropol.* 51: 39-44.

Odhiambo Nengo, I. and Rae, T.C. (1992) New hominoid fossils from the early Miocene site of Songhor, Kenya. *J. Hum. Evol.* 23: 423-429.

Oxnard, C.E. (1963) Locomotor adaptations in the primate forelimb. *Symp. Zool. Soc. Lond.* 10: 165-182.

Oxnard, C.E., Crompton, R.H. and Lieberman, S.S. (1990) *Animal Lifestyles and Anatomies: the Case of the Prosimian Primates.* University of Washington Press: Seattle.

Oxnard, C.E. and Lisowski, F.P. (1980) Functional articulation of some hominoid foot bones: implications for the Olduvai (Hominid 8) foot. *Am. J. Phys. Anthropol.* 52: 107-117.

Pilbeam, D. (1969) Possible identity of Miocene tali from Kenya. *Nature* 223:648.

Pilbeam, D. (1997) Research on Miocene hominoids and hominid origins: the last three decades. In D.R. Begun, C.V. Ward and M.D. Rose (eds.) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 13-28. Plenum Press: New York.

Preuschoft, H. (1973) Body posture and mode of locomotion in some East African Miocene Dryopithecinae. In M.H. Day (ed.) *Human Evolution: Symp. for the study of Hum. Biol. XI*, pp. 13-46.

Prost, J.H. (1965) A definitional system for the classification of primate locomotion. *Amer. Anthropol.* 67: 1198-1214.

Prost, J.H. (1965) Origin of bipedalism. *Am. J. Phys. Anthropol.* 52: 175-189.

Rae, T.C. (1993) *Phylogenetic Analysis of Proconsulid Facial Morphology.* Ph.D. dissertation, State University of New York at Stony Brook.

Rae, T.C. (1999) Mosaic evolution in the origin of the Hominoidea. *Folia Primatol.* 70: 125-135.

Richard, A. (1970). A comparative study of the activity patterns and behaviour of *Alouatta villosa* and *Ateles geoffroyi. Folia Primatol.* 12: 241-263.

Richmond, B.G., Fleagle, J.G., Kappelman, J. and Swisher, C.C. (1998) First hominoid from the Miocene of Ethiopia and the evolution of the catarrhine elbow. *Am. J. Phys. Anthropol.* 105: 257-277.

Rollinson, J. and Martin, R.D. (1981) Comparative aspects of primate locomotion, with special reference to arboreal cercopithecines. *Symp. Zool. Soc. Lond.* 48: 377-427.

Rose, M.D. (1983) Miocene Hominoid postcranial morphology: monkey-like, ape-like, neither or both? In R. Ciochon and R. Corruccini (eds.) *New Interpretations of Ape and Human Ancestry,* pp.405-417. Plenum Press: New York.

Rose, M.D. (1988) Another look at the anthropoid elbow. *J. Hum. Evol.* 17: 193-224.

Rose, M.D. (1989) New postcranial specimens of catarrhines from the Middle Miocene Chinji formation, Pakistan: descriptions and a discussion of proximal humeral functional morphology in anthropoids. *J. Hum. Evol.* 18: 131-162.

Rose, M.D. (1992) Kinematics of the trapezium-first metacarpal joint in extant anthropoids and Miocene hominoids. *J. Hum. Evol.* 22: 255-266.

Rose, M.D. (1996) Functional morphological similarities in the locomotor skeleton of Miocene catarrhines and platyrrhine monkeys. *Folia Primatol.* 66: 7-14.

Rose, M.D. (1997) Functional and phylogenetic features of the forelimb in Miocene hominoids. In D.R. Begun, C.V. Ward and M.D. Rose (eds.) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations,* pp. 79-100. Plenum Press: New York and London.

Rose, M.D., Leakey, M.G., Leakey, R.E.F. and Walker, A.C. (1992) Postcranial specimens of *Simiolus enjiessi* and other primitive catarrhines from the early Miocene of Lake Turkana, Kenya. *J. Hum. Evol.* 22: 171-237.

Ruff, C.B., Walker, A. and Teaford, M.F. (1989) Body mass, sexual dimorphism and femoral proportions of *Proconsul* from Rusinga and Mfangano Islands, Kenya. *J. Hum. Evol.* 18: 515-536.

Runestad, J.A (1997) Postcranial adaptations for climbing in Lorisidae (Primates). *J. Zool., Lond.* 242: 291-297.

Sanders, W.J. and Bodenbender, B.E. (1992) Morphometric analysis of lumbar vertebra UMP 67-28: implications for spinal function and phylogeny of the Miocene Moroto hominoid. *J. Hum. Evol.* 26: 203-237.

Sarmiento, E.E. (1988) Anatomy of the hominoid wrist joint: its evolutionary and functional implications. *Int. J. Primatol.* 9(4): 281-345.

Sarmiento, E.E. (1994) Terrestrial traits in the hands and feet of gorillas. *Am. Mus. Novitates* 3091. American Museum of Natural History: New York.

Sarmiento, E.E. (1998) Generalised quadrupeds, commited bipeds, and the shift to open habitats: an evolutionary model of hominid divergence. *Am. Mus. Novitates* 3250. American Museum of Natural History: New York.

Schmitt, D. (1998) Forelimb mechanics during arboreal and terrestrial quadrupedalism in Old World Monkeys. In E. Strasser, J. Fleagle, A. Rosenberger and H. McHenry (eds.) *Primate Locomotion: Recent Advances*, pp. 175-200. Plenum Press: New York.

Schmitt, D. and Larson, S.G. (1995) Heel contact as a function of substrate type and speed in primates. *Am. J. Phys. Anthropol.* 96: 39-50.

Schon Ybarra, M.A. (1998) Arboreal quadrupedalism and forelimb articular anatomy of Red Howlers. *Int. J. Primatol.* 19(3): 599-613.

Schon Ybarra, M.A. and Conroy, G.C. (1978) Non-metric features in the ulna of *Aegyptopithecus*, *Alouatta*, *Ateles* and *Lagothrix*. *Folia Primatol.* 29: 178-195.

Schon, M.A. and Zeimer, L.K. (1973) Wrist mechanism and locomotor behaviour of *Dryopithecus (Proconsul) africanus*. *Folia Primatol.* 20: 1-11.

Smith, R.J. and Pilbeam, D.R. (1980) Evolution of the orangutan. *Nature* 284: 44-45.

Spoor, C.F., Sondaar, P.Y. and Hussain, S.T. (1991) A new hominoid hamate and first metacarpal from the Late Miocene Nagri Formation of Pakistan. *J. Hum. Evol.* 21: 413-424.

Strait, D.S., Richmond, B.G. and Polk, D.J (2000) The locomotor anatomy of hominoid and hominid ancestors. *Am. J. Phys. Anthropol. Suppl.* 30: 294.

Strasser, E (1988) Pedal evidence for the origin and diversification of cercopithecid clades. *J. Hum. Evol.* 17: 225-245.

Tattersall, I. (1982) *The Primates of Madagascar*. Columbia University Press: New York.

Tuttle, R. (1967) Knuckle-walking and the evolution of the hominoid hand. *Am. J. Phys. Anthropol.* 26: 171-206.

Tuttle, R. (1969) Knuckle-walking and the problem of human origins. *Science* 166: 953-961.

Tuttle, R.H. (1986) *Apes of the World: their Social Behaviour, Communication, Mortality and Ecology*. Noyes Publications: New Jersey.

Walker, A. (1969) The locomotion of the lorises, with special reference to the potto. *E. Afr. Wildlife Journal* 7: 1-5.

Walker, A. (1997) *Proconsul*: function and phylogeny. In D.R. Begun, C.V. Ward and M.D. Rose (eds.) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations*, pp. 209-224. Plenum Press: New York.

Walker, A.C. and Pickford, M. (1983) New postcranial fossils of *Proconsul africanus* and *Proconsul nyanzae*. In R.L. Ciochon and R.S. Corruccini (eds.) *New Interpretations of Ape and Human Ancestry*, pp.325-351. Plenum Press: New York.

Walker, A. and Rose, M.D. (1968) Fossil hominoid vertebra from the Miocene of Uganda. *Nature* 217: 980-981.

Walker, A., Teaford, M.F., Martin, L. and Andrews, P. (1993) A new species of *Proconsul* from the early Miocene of Rusinga/Mfangano Islands, Kenya. *J. Hum. Evol.* 25: 43-56.

Walker, S.E. (1998) Fine grained differences within positional categories: a case study of *Pithecia* and *Chiropotes*. In Strasser et al. (eds.) *Primate Locomotion: Recent Advances*, pp.31-43. Plenum Press, New York.

Walker, S.E. and Ayres, J.M. (1996) Positional behaviour of the white uakari (*Cacajao calvus calvus*). *Am. J. Phys. Anthropol.* 101: 161-172.

Ward, C.V. (1993a) Function and phylogeny in hominoid trunk and hindlimb evolution. *Am. J. Phys. Anthropol. Suppl.* 16: 204.

Ward, C.V. (1993b) Torso morphology and locomotion in *Proconsul nyanzae*. *Am. J. Phys. Anthropol.* 92: 219-328.

Ward, C.V. (1997) Functional anatomy and phyletic implications of the hominoid trunk and hindlimbs. In D.R. Begun, C.V. Ward and M.D. Rose (eds.)

Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations, pp. Plenum Press: New York.

Ward, C.V. (1998) *Afropithecus*, *Proconsul* and the primitive hominoid skeleton. In E. Strasser, J. Fleagle, A. Rosenberger and H. McHenry (eds.) *Primate Locomotion: Recent Advances*, pp. 337-352. Plenum Press: New York.

Ward, C.V., Ruff, C.R., Walker, A., Teaford, F., Rose, M.D. and Nengo, I.O. (1995) Functional morphology of *Proconsul* patellas from Rusinga Island, Kenya, with implications for other Miocene-Pliocene catarrhines. *J. Hum. Evol.* 29: 1-19.

Ward, C.V., Walker, A. and Teaford, M.F. (1991) *Proconsul* did not have a tail. *J. Hum. Evol.* 21: 215-220.

Ward, C.V., Walker, A., Teaford, M.F. and Odhiambo, I. (1993) Partial skeleton of *Proconsul nyanzae* from Mfangano Island, Kenya. *Am. J. Phys. Anthropol.* 90: 77-111.

Ward, C.V., Begun, D.R. and Rose, M.D. (1997) Function and phylogeny in Miocene hominoids In D.R. Begun, C.V. Ward and M.D. Rose (eds.) *Function, Phylogeny and Fossils: Miocene Hominoid Evolution and Adaptations,* pp. 1-12. Plenum press: New York.

Wood, B.A. (1973) Locomotor affinities of hominoid tali from Kenya. *Nature* 246: 45-46.

Youlatos, D. (1996) Atelines, apes and wrist joints. *Folia Primatol.* 67: 193-198.

Zihlman, A.L. (1992) Locomotion as a life history character: the contribution of anatomy. *J. Hum. Evol.* 22: 315-325.

Zwell, M. and Conroy, G.C. (1973) Multivariate analysis of the *Dryopithecus africanus* forelimb. *Nature* 244: 373-375.